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Observed, predicted and simulated responses from reciprocal recurrent selection in maize (*Zea mays* L.)

by

John Munson Martin

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INTRODUCTION

Much of maize (Zea mays L.) breeding methodology is centered around improving and maintaining genetically variable populations to be used as source material for parental inbred lines. The general breeding method is called "population improvement". The underlying assumption is that hybrid improvement is proportional to improvement in the source populations from which the parental inbred lines were derived.

Jenkins (1940) outlined procedures for population improvement. It entailed crossing plants from the source population to a broad-base tester, evaluating the testcross progenies, and then recombining the superior genotypes. The process could be repeated by recurring cycles of selection; thus, the term recurrent selection has been applied to these procedures. Hull (1945) proposed that an inbred line or single-cross be used as the tester; he called this procedure recurrent selection for specific combining ability. Comstock, Robinson, and Harvey (1949) proposed a further modification of the general procedure to permit the simultaneous, reciprocal improvement of two source populations to maximize performance of the population cross. This was accomplished by using each population as a tester for the other. Comstock et al.'s (1949) modification is now known as reciprocal recurrent selection.

A reciprocal recurrent selection program in maize was

initiated in 1949 at the Iowa Agriculture and Home Economics Experiment Station by G. F. Sprague. The two source populations were Iowa Stiff Stalk Synthetic and Iowa Corn Borer Synthetic #1. The objective of this study is to evaluate observed and predicted responses for grain yield and other important agronomic traits in the two source populations and their crosses after seven cycles of reciprocal recurrent selection. Computer simulation will be used to gain insight into the genetic model operating in the two source populations being studied.

LITERATURE REVIEW

Lonnquist (1961) has defined recurrent selection as:

> The common procedure followed in any improvement program where selected genotypes from a heterogeneous population are ultimately intercrossed to form a new segregating population for another cycle of selection.

The genetic worth of genotypes can be judged on an individual or progeny mean basis. The discussion here will be confined to recurrent selection methods where the selection units are half-sib family means.

Recurrent Selection Methods

Jenkins (1940) described a method for developing improved maize varieties. This procedure is now termed recurrent selection for general combining ability. Sprague and Tatum (1942) defined "general combining ability" as the average performance of a line in hybrid combinations. On the other hand, "specific combining ability" described the specific hybrid combinations which performed relatively better or worse than the average. The important steps in Jenkins' procedure are as follows:

1. Season one: isolate one generation selfed (S_1) lines, and cross the selfed plants to several "tester" plants to form testcrosses.
2. Season two: evaluate the testcrosses in replicated yield trials.
3. Season three: intercross the best S_1 lines to form the new synthetic variety.

4. Repeat the above steps.

The parental variety was suggested as the tester in step 2. Jenkins also stated "about 10" lines should be selected and recombined to form the new synthetic variety.

The original objective of this method was to use it as a means of producing improved synthetic varieties for marginal maize growing areas. The justification for the procedure arose from earlier work where Jenkins (1935) found lines became stable for yield early in the inbreeding process. Thus, Jenkins concluded superior genotypes could be identified in hybrid combinations with little or no selfing.

Hull (1945) modified Jenkins' original recurrent selection scheme by proposing that an inbred line or single-cross be used as the tester for the source population. He called his method recurrent selection for specific combining ability. The essential steps in recurrent selection for specific combining ability are as follows:

1. Season one: self-pollinate at least 100 plants in the source population and cross each separately to several inbred tester plants.
2. Season two: evaluate the testcrosses in replicated yield trials.
3. Season three: recombine 10 or more of the superior selfed lines to form the new source population.
4. Repeat the above steps.

Hull considered the choice of the inbred tester a crucial

decision. He suggested using an inbred with proven parental value in hybrid combinations. Then, as inbreds were isolated from the source population, they could be used in hybrid combinations with the tester line as single-crosses or as a parent in double-crosses to be grown commercially.

The essential difference between Jenkins' and Hull's methods is the tester used when forming the testcrosses. This difference can be rationalized by considering each author's views as to the cause of yield heterosis. Jenkins believed hybrid vigor was a function of the number of dominant favorable alleles contributed by each parent. Whereas, Hull thought hybrid vigor was the result of nonlinear interactions of genes at different loci (epistasis) and/or among alleles at the same locus (overdominance). Thus, Jenkins believed the parental tester would make for an accumulation of dominant favorable alleles in the source population. Likewise, Hull believed the inbred tester technique would identify superior hybrid combinations among genes and alleles.

Noting the conflict between the two methods cited earlier, Comstock, Robinson, and Harvey (1949) proposed a breeding method designed to exploit both general and specific combining ability. This method is now called reciprocal recurrent selection, and the basic procedures are as follows:

1. Season one: cross about 200 plants from source population A to four or five random plants from source population B. Likewise, cross about 200

plants from source population B to four or five random plants from source population A. Self-pollinate all plants used as pollen parents.

2. Season two: evaluate the two sets of testcrosses in separate yield trials.
3. Season three: recombine the superior S_1 lines using the selfed seed to form the new populations.
4. Repeat the above steps.

Comstock et al. (1949) proposed that the two source populations could be two open-pollinated varieties, two synthetics, or two F_2 populations of a single-cross each used as a parent in a successful double-cross. But in all cases the authors stressed the two populations should be chosen to be as genetically diverse as possible.

Comstock et al. (1949) listed several possible uses for reciprocal recurrent selection in commercial maize production. For example, the variety hybrid cross could be released directly for use by the farmers, or double-crosses of the form $(A_1xA_2)(B_1xB_2)$ could be produced where A_1 and A_2 are inbreds isolated from source population A, and B_1 and B_2 are inbreds from source population B.

Both Jenkins' (1940) and Hull's (1945) methods are intrapopulation procedures. The objective is to improve the source population itself. In contrast reciprocal recurrent selection is an interpopulation improvement method. That is, both source populations are improved so as to maximize the cross

between them.

Progress from Selection

The objective of any breeding procedure is to make genetic improvement in the target population. Selection methods differ in their expected rate of genetic advance. Both rate and total amount of genetic improvement are dependent upon genetic parameters in the selection population(s). Before prediction equations can be examined, some definitions must be introduced. Much of the notation and ideas that follow are taken from Comstock et al. (1949) and Empig, Gardner, and Compton (1972).

It is convenient to express genotypes, genotypic values, and their associated frequencies for a one locus model in the following way.

Genotype	Frequency	Genotypic value (Y)	Frequency of favorable allele (X)
AA	p^2	u	1
Aa	2pq	au	1/2
aa	q^2	-u	0

u is one-half the difference between the two homozygous genotypes, and a denotes the level of dominance. For example, a = 0 and a = 1 specifies the case for no dominance and complete dominance, respectively.

The mean of the population, $\bar{g}$, is

$$p^2u + 2pqau - q^2u = (p-q)u + 2pqau \quad .$$

The mean frequency of the favorable allele is $p^2 + 2pq\frac{1}{2}$, which simplifies to p. The total genetic variance, σ_g^2, is

$$p^2u^2 + 2pqa^2u^2 + q^2u^2 - \bar{g}^2 \quad .$$

The additive genetic variance, σ_A^2, is defined as the sum of squares due to regression of genotypic value, Y, on number of favorable alleles, X. Because the sums of squares removed by regression is $\frac{Cov(X,Y)^2}{\sigma_X^2}$, σ_A^2 is

$$\frac{p^2u\,1 + 2pqau\,\frac{1}{2} - p[(p-q)u + 2pqau]^2}{p^2 + 2pq\frac{1}{4} - p^2}$$

which after simplification is

$$2pq[1 + (1-2p)a]^2\,u^2 \quad .$$

Finally dominance variance $\sigma_D^2 = \sigma_g^2 - \sigma_A^2$, or

$$4p^2q^2a^2u^2 \quad .$$

All calculations that follow are subject to the following assumptions:

1. Random mating base populations,
2. Normal diploid meiosis,
3. No multiple alleles,
4. No interaction among loci (or no epistasis),
5. Independent assortment among genes (or linkage equilibrium),
6. No correlation between genotype and environment, and
7. No inbreeding.

Using these assumptions all parameters can be extended to any number of loci by summing over all loci. For example, the population mean $\bar{g}$ would be

$$\sum_{i=1}^{n} [(p_i - q_i)u + 2p_i q_i au] \quad .$$

From the equation describing the population mean it is evident that the population mean is dependent on gene frequencies. Selection affects a change in the population mean by changing gene frequencies.

Expected genetic progress, ΔG_i, at the i^{th} locus is the product of the change in gene frequency, Δp_i, per unit change in phenotypic value, P, and the change in mean genotypic value per unit change in gene frequency; i.e.,

$$\Delta G = \Delta p_i \frac{d\bar{g}_i}{dp_i} \quad .$$

Δp_i can be written as $(S\beta p_i, P)$, where S is the selection differential and $\beta p_i, P$ is the regression coefficient of gene frequency in the selection unit on phenotypic value in the selection unit. Then

$$\beta p_i, P = \frac{Cov(p_i, P)}{\sigma_p^2}$$

with σ_p^2 being the phenotypic variance among selection units. But since genotypic and phenotypic values are assumed uncorrelated,

$$\frac{\text{Cov}(p_i,P)}{\sigma_p^2} = \frac{\text{Cov}(p_i,Y)}{\sigma_p^2}$$

where Y is genotypic value. Substituting for Δp_i,

$$\Delta G_i = \frac{S\ \text{Cov}(p_i Y)}{\sigma_p^2} \frac{d\bar{g}_i}{dp_i} \quad .$$

Now summing over all loci

$$\Delta G = \frac{S}{\sigma_p^2} \sum_{i=1}^{n} \text{Cov}(p_i,Y) \frac{d\bar{g}_i}{dp_i} \quad .$$

Predicted gain from half-sib testing with an unrelated, broad genetic based tester (recurrent selection for general combining ability) and reciprocal recurrent selection will be derived to illustrate the use of the above expressions. The selection unit in both situations is the half-sib family. Let p be the frequency of the more favorable allele in the population to be improved and r denote the same in the tester population. Also $q = (1-p)$ and $s = (1-r)$.

From Table 1 the mean of the testcrosses, $\bar{g}_T$, is

$$p^2(ru+sau) + 2pq\tfrac{1}{2}[(r-s)u + au] + q^2(rau-su) =$$
$$[(pr-qs) + a[p + r(q-p)]]u \quad .$$

Similarly, the mean frequency of the favorable allele is

$$p^2 + 2pq\tfrac{1}{2} = p \quad .$$

The change in mean value per unit change in gene frequency in the selection population can be expressed mathematically as

$$\frac{d}{dp}[(p-q)u + 2pqau] = 2[1 + (1-2p)a]u \quad .$$

Table 1. Selection and testcross arrays for half-sib testing with an unrelated tester

Selection genotype	Frequency	Frequency of favorable (X)	Testcross genotypes (Y)	Frequency of Y	Genotypic value	Mean of half-sib families
AA	p^2	1	AA	r	u	u(r+sa)
			Aa	s	au	
Aa	2pq	1/2	AA	r/2	u	
			Aa	1/2	au	
			aa	s/2	-u	$\frac{u}{2}$(r-s+a)
aa	q^2	0	Aa	r	au	u(ra-s)
			aa	s	-u	

The second term in the prediction equation, Δp_i, is

$$\frac{S\ Cov(X,Y)}{\sigma_p^2} \quad .$$

$$Cov(X,Y) = p^2[ru+sau] + 2pq\tfrac{1}{2}[(r-s)u + au] - p[(pr-qs) + a[p+r(q-p)]]u = \frac{pq}{2}(r+s)u + [p^2(s+r-1) + pq(\tfrac{1}{2}-r)]au =$$

$$\frac{pq}{2}[1+(s-r)a]u \quad .$$

Making the proper substitutions, ΔG becomes

$$\frac{S}{\sigma_p^2}\ \frac{pq}{2}[1+(s-r)a]u\ 2[1+(q-p)a]u \quad .$$

If $\alpha^T = [1+(q-p)a]u$ and $\alpha^A = [1+(s-r)a]u$, the ΔG for half-sib testing can be written more simply as

$$\frac{S}{\sigma_p^2}\ pq\alpha^A\alpha^T \text{ and summing over all loci}$$

$$\Delta G = \frac{S}{\sigma_p^2} \sum_{i=1}^{n} p_i q_i\ \alpha_i^A\ \alpha_i^T \quad .$$

The reciprocal recurrent selection case is equivalent to the half-sib testing case if each population is considered as the tester for the other. However, in this instance, predicted gain refers to hybrid improvement and not to the populations themselves. Let p be the frequency of the more favorable allele in source population A, and similarly let r be the frequency of the more favorable allele in population B. If genotypes are chosen truly at random, the mean of the test-crosses is the mean of the variety hybrid cross, $\bar{X}$, which is

$$[(pr-qs) + a[p + r(q-p)]u = [p(1+a) + r(1+a) - 2pra]u \quad .$$

If selection changes p to $p+\Delta p$ and r to $r+\Delta r$, then the mean of the hybrid after selection, $\bar{X}'$, is

$$[(p+\Delta p)(1+a) + (r+\Delta r)(1+a) - 2(p+\Delta p)(r+\Delta r)a]u \quad .$$

Ignoring terms involving both Δp and Δr, the change in the hybrid mean due to selection is

$$\bar{X}'-\bar{X} = [\Delta p(1+a) + \Delta r(1+a) - 2ar\Delta p - 2ap\Delta r]u \quad .$$

The expressions Δp and Δr can be obtained exactly as in the half-sib testing case. The necessary calculations give:

$$\Delta p = \frac{S}{\sigma_p^2} pq[1+(s-r)a]u = \frac{S}{\sigma_p^2} pq\alpha^B, \quad \text{and}$$

$$\Delta r = \frac{S}{\sigma_p^2} rs[1+(q-p)a]u = \frac{S}{\sigma_p^2} rs\alpha^A \quad .$$

After substituting expressions for Δp and Δr into the above formulae, the expected change in hybrid performance reduces to

$$\Delta G = \frac{S}{\sigma_p^2} \tfrac{1}{2}[pq(\alpha^B)^2 + rs(\alpha^A)^2] \quad .$$

Finally, summing over all loci,

$$\Delta G = \frac{S}{\sigma_p^2} \tfrac{1}{2} \sum_{i=1}^{n} [p_i q_i (\alpha_i^B)^2 + r_i s_i (\alpha_i^A)^2]$$

Griffing (1962) gave expressions for predicted genetic advance for all mating systems involving two source populations. Reciprocal recurrent selection is a special case of the general mating system. He extended the prediction formulae to include multiple alleles and examined the effect of linkage

and epistasis on genetic improvement. His conclusion was that permanent genetic gains were a function of only the additive genetic variances and covariances in the source populations.

Theoretical comparisons of recurrent selection for general combining ability (method 1), recurrent selection for specific combining ability (method 2), and reciprocal recurrent selection (method 3) were presented by Comstock et al. (1949). The authors considered limits to improvement as well as rates of improvement. When limits to improvement were compared, three conclusions were listed. First, when $a < 1.0$ (partial dominance) methods 1 and 3 were essentially equivalent, Method 2 could attain the same maximum limit only if the favorable allele were present in both the source population and the tester line. Second, the improvement limit for methods 2 and 3 would be the same and superior to method 1 for $a > 1.0$ (overdominance). Finally, with no dominance ($a = 0.0$) all three methods had the same limits for improvement.

When rate of improvement was considered, Comstock et al. (1949) also listed three conclusions. With complete dominance method 3 yielded an initial advantage over the other two methods. But with further cycles of selection, method 1 showed the fastest rate of improvement. With partial dominance the situation was similar to the complete dominance case, except the initial advantage for method 3 was not as great. If the tester line used in method 2 had a low frequency of the favorable allele, method 1 would have a greater rate of im-

provement in the long run than method 2 or method 3. Comstock et al. (1949) summarized that reciprocal recurrent selection was almost as effective as either of the other two methods for all genetic situations considered.

Originally, reciprocal recurrent selection was proposed as a breeding method that would capitalize on both general and specific combining ability. Schnell (1961) pointed out that Sprague and Tatum's (1942) definitions of general and specific combining ability need not be restricted to homozygous genotypes and could be extended to include heterozygous material as well. He emphasized reciprocal recurrent selection does not make use of specific combining ability, since it does not select for specific hybrid genotypes. It does take advantage of specific combining ability only if one assumes that the two source populations are members of a large super population comprised of all populations available.

Cress (1966) compared rates of improvement from reciprocal recurrent selection with recurrent selection within the two separate source populations (within population selection). The approach was to use the comparison C = abMba - $\frac{1}{2}$(aaMaa + bbMbb) where abMba, aaMaa, and bbMbb represent theoretical gains from reciprocal recurrent selection, recurrent selection within population A, and recurrent selection within population B, respectively. A positive C indicated more rapid progress from abMba, whereas a negative C meant rate of progress was greater in aaMaa and bbMbb. It was found that

reciprocal recurrent selection gave a greater rate of improvement than within population selection for all levels of dominance when the sum of the frequency of the favorable allele in populations A and B (a+b) was less than 1.0. On the other hand, within population selection was best for partial to complete dominance if a + b > 1.0. The general conclusion was that for partial to complete dominance rate of improvement from reciprocal recurrent selection would be superior to within population selection only for a few cycles; that is, until a + b becomes greater than one.

Cress (1967) used computer simulation to study progress from reciprocal recurrent selection (RRS) as proposed by Comstock et al. (1949) and two modifications of the original procedure. The first modification was to complete one generation of selfing in the populations before forming the testcrosses (RRS_S); the second was to use the original populations as a constant tester throughout selection (RRS_C). Each simulated population contained 90 individuals each with 40 independently segregating loci, and the 10 superior individuals were recombined to form the new populations. Twenty cycles of selection were simulated for each method. Response from selection was compared for overdominance and complete dominance at each of several starting gene frequencies in the original populations.

For complete dominance the results indicated total genetic advance in the hybrid population was about equal for

the three methods after 20 cycles of selection. But rate of gain during the first few cycles was greater for the RRS_S method. All three methods produced similar but small increases in the populations themselves. Hybrid response was about the same for RRS and RRS_S with overdominance, but the RRS_C method gave no improvement in hybrid performance. For hybrid performance to improve with overdominance, the populations must be improved complementary to each other. With the constant tester method this was not allowed to occur.

Results from computer simulation and the study cited earlier prompted Cress (1967) to suggest two conditions to ensure both maximum genetic potential and rapid rate of progress from recurrent selection. First, all genetic material should be combined into one synthetic before initiation of selection. Any subpopulations needed should be taken as subsamples from the large population. This would ensure that all useful alleles would be present in the subpopulations. Also, one generation of selfing should precede the testcrosses.

Jones, Compton, and Gardner (1971) compared half-sib and full-sib reciprocal recurrent selection via computer simulation. Full-sib reciprocal recurrent selection showed a higher rate of improvement for all genetic situations studied. The selection intensities, however, were 25% and 50% for full-sib and half-sib reciprocal recurrent selection, respectively.

With populations that are infinitely large, selection

would be expected to increase the frequency of the favorable alleles until they eventually become fixed. In practice, breeding populations are finite and gene frequencies are subject to random changes from one generation to the next. Thus, in small populations some favorable alleles may be lost due to random genetic drift. Kimura (1957) has quantified the probability of chance fixation of an allele as

$$P = \frac{1-e^{-2Nsq}}{1-e^{-2Ns}} \quad .$$

q is the initial frequency of the allele, s is the selective advantage of the allele, and N is the effective population size.

Robertson (1960) has pointed out that in artificial selection there are two opposing forces operating on gene frequencies. On the one hand, some favorable alleles may be lost due to genetic drift. Selection operates in the opposite direction to increase the frequency of favorable alleles. In essence, this means the full genetic potential in a population may never be realized because of chance fixation of favorable alleles.

Comstock (1977) stated one of the requirements for success from any recurrent selection system is that effective population size should be "sufficient to trivialize the ultimate consequences of genetic drift." He further suggested a reasonable basis for theoretical comparisons among recurrent selection systems would be:

1. Expected change in mean value per unit time,
2. Operation cost, and
3. The product Ns where N is the effective population size and s is the selective advantage of the allele.

Empirical Results from Recurrent Selection

Lonnquist (1961) has summarized several selection experiments from Nebraska using two open-pollinated varieties, Krug and Reid, and three synthetic varieties, Stiff Stalk Synthetic, Synthetic A, and Synthetic B. After three cycles of recurrent selection for general combining ability, the improved varieties showed an average increase of 7.2 q/ha over the original (C_0) populations. To assess the changes in combining ability associated with selection, all possible intercrosses of the populations were evaluated. Three cycles of selection produced a mean increase of 7.2 q/ha over the original $\bar{C}_0 x \bar{C}_0$ crosses. Lonnquist attributed the improvement in the populations themselves to an accumulation of favorable alleles having additive effects. He also noted improvement in the varieties had not altered yield heterosis among them.

Four cycles of recurrent selection for general combining ability in Iowa Stiff Stalk Synthetic (BSSS) using the double-cross Ial3 as tester were summarized by Penny et al. (1963). Yield improvement when crossed to the Ial3 tester was only 1.2% per cycle. But after seven cycles of

selection Eberhart, Debela, and Hallauer (1973) reported gains of 1.6 q/ha and 1.08 q/ha per cycle for BSSS(HT) in crosses with Ial3 and an unrelated tester, respectively. However, the actual gain was much less than the predicted 3.17 q/ha per cycle gain expected from selection with the Ial3 tester. Similarly, the BSSS population itself was improved 0.74 q/ha per cycle despite an estimated 29% inbreeding after the seventh cycle.

Genter and Eberhart (1974) evaluated several original (C_0) and improved (Cn) populations in a diallel crossing arrangement. The $BSSSC_0$ population had the best general combining ability and highest heterosis among the original populations. But in contrast to the previous study mentioned $BSSS(HT)C_7$ expressed little if any improvement in combining ability in hybrid combinations. The authors cited instances where the same breeding method produced improvement in one population and not in another. Genotype x environment interaction and differing germplasm bases among the populations were suggested as possible reasons for the inconsistencies.

In Florida, Horner et al. (1973) conducted recurrent selection using the parental variety and an inbred line as testers. After five cycles of selection all selected populations were crossed to the original population and to an unrelated tester. The inbred tester method had almost twice as much improvement in grain yield as the parental tester method (2.20 q/ha versus 1.19 q/ha per cycle). The selection

populations themselves showed a quadratic response over five cycles of selection; that is, there was a decline in yield for two cycles followed by an increase thereafter.

Russell, Eberhart, and Vega (1973) evaluated five cycles of recurrent selection in two populations, Alph and (WF9xB7)F_2. The inbred, B14, was used as the tester for both populations. They observed significant rates of improvement for grain yield in the populations themselves. When the selected populations from Alph and (WF9xB7)F_2 were crossed to B14 and to BSBB, an unrelated broad-base tester, rates of yield improvement were essentially parallel for both testers.

In a similar study, Walejko (1976) evaluated five cycles of recurrent selection for specific combining ability in Kolkmeier and Lancaster populations using the inbred, Hy, as the tester for both populations. No significant, positive yield gain was noted for either population. Significant improvement in yield was found in the Hy x Kolkmeier Cn and Hy x Lancaster Cn testcrosses. Equal rates of improvement were expressed when the selected populations were in testcrosses with other unrelated testers.

All studies regarding recurrent selection for specific combining ability have reached similar conclusions. First, inbred testers have been successful in improving source populations for general combining ability as evidenced by the fact that yield gains have been equally well-expressed in hybrid combinations with the inbred tester and unrelated

testers. This result is cited as evidence that over-dominance type gene action is not of major importance in conditioning yield in maize.

Douglas et al. (1961) used reciprocal recurrent selection to improve Ferguson's Yellow Dent and Surecropper maize populations. Three cycles of selection produced a significant improvement in yield in Ferguson's Yellow Dent, but Surcropper showed no significant change. The average combining ability of both populations was improved with respect to the original varieties.

Two cycles of reciprocal recurrent selection improved grain yield, popping volume, and lodging resistance in two popcorn varieties (Thomas and Grissom, 1961). Selection of S_1 lines to be recombined was based on an index where yield and popping volume were weighted twice as much as lodging score.

Moll and Robinson (1966) and Moll and Stuber (1971) have compared reciprocal recurrent selection in Jarvis and Indian Chief with full-sib family selection within the same populations. Following six cycles of selection with each method full-sib family selection produced 3.5% and 2.8% yield gain in Jarvis and Indian Chief, respectively. Jarvis showed a 2.3% yield increase per cycle with reciprocal recurrent selection, but Indian Chief indicated no significant change in yield with the same method. Hybrid improvement among selected populations ($C_0 x C_0$ to CnxCn crosses) was 3.5% per

cycle for reciprocal recurrent selection and 2.5% per cycle for full-sib family selection. It should be noted that full-sib family selection was favored slightly in that selection intensities were 9.8% and 13.3% for full-sib and reciprocal recurrent selection, respectively. Estimates of predicted gain were calculated using variance component estimates from the testcross yield trials for each method. The expected gains were in reasonably good agreement in all instances.

Darrah, Eberhart, and Penny (1972) reported 3.3 q/ha per cycle increase in grain yield following two cycles of reciprocal recurrent selection in two maize populations in Kenya. One of the populations showed a significant yield improvement, but the other did not show any response to selection.

A reciprocal recurrent selection program has been in progress in Iowa since 1949 with Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic #1 (BSCB1). Penny and Eberhart (1971) summarized the first four cycles of selection and found only 1.7% per cycle improvement in hybrid performance for grain yield compared with a predicted gain of 7.2% per cycle. Citing the disappointing improvement from selection Penny and Eberhart (1971) suggested changes for subsequent cycles of selection. The first was to select pollen parents from among S_1 plants (each derived from a different S_0 plant) rather than from among S_0 plants. This change would permit selection among S_1 lines for agronomic traits. Also, the

generation of selfing should increase the variation among the testcross entries (Horner, 1968). The second change was to base selection on yield harvested with a machine harvester rather than on yield "produced".

Eberhart, Debela, and Hallauer (1973) evaluated seven cycles of half-sib selection in BSSS and five cycles of reciprocal recurrent selection in the BSSS and BSCB1 populations. Significant yield improvement was not obtained in either the BSSS(R) or the BSCB1(R) populations themselves. In contrast the BSSS(HT) population showed a 0.74 q/ha per cycle increase in yield. BSSS(R)Cn x BSCB1(R)Cn and BSSS(HT)Cn x BSCB1(R)Cn populations crosses exhibited yield increases of 2.73 q/ha and 2.31 q/ha per cycle, respectively. Heterosis from the C_0xC_0 to C_5xC_5 crosses was more than doubled for both selection methods. Rates of improvement were found to be higher in this study than had been reported previously by Penny and Eberhart (1971). Reasons cited for this discrepancy were sampling errors and genotype x environment interaction.

Russell and Eberhart (1975) compared line x line crosses among groups of five selected S_2 lines from BSSS(R)C_5 and BSCB1(R)C_5 selection populations and S_2 or S_3 lines from the BSSS(HT)C_6 selection population with their respective population cross means. The five lines in each instance were five of the 10 lines to be recombined to form the new selection populations. The three sets of 25 line x line crosses, the

population crosses, and several single-cross hybrid checks were evaluated in the same experiment. Most of the variation for yield within sets of crosses could be attributed to average performance of lines (general combining ability). Furthermore, 19 BSSS(R) x BSCB1(R), 10 BSSS(HT) x BSCB1(R), and five BSSS(R) x BSSS(HT) crosses significantly exceeded their respective population crosses. Compared with the highest yielding single-cross check (B37xOh43), two BSSS(R) x BSCB1(R) crosses yielded significantly more, and none of the crosses in the set yielded significantly less than the best check hybrid. Russell and Eberhart (1975) cited these results as evidence recurrent selection methods and reciprocal recurrent selection in particular can be an efficient means of producing high yielding commercial single-cross hybrids.

MATERIALS AND METHODS

Genetic Materials

All entries evaluated in this study were either original or improved synthetic maize populations of Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic #1 (BSCB1). BSSS was synthesized from 16 inbred lines selected for their superior stalk strength. BSCB1 was synthesized from 12 inbred lines which showed good resistance to European corn borer (Ostrinia nubilalis Hübner) feeding at the time of synthesis. All lines in both synthetic varieties were of U.S. origin and Corn Belt maturity. Table 2 lists the inbred lines making up both synthetic varieties.

In this study the C_0, C_1, C_3, C_5, and C_7 populations from BSSS(R) and BSCB1(R) along with the C_0xC_0, C_5xC_5, and C_7xC_7 population crosses from the reciprocal recurrent selection program were evaluated. The R designates reciprocal recurrent selection. In addition, BSSS(M)C_6 and BS13 were included to bring the total number of entries to 15. BSSS(M)C_6 is BSSS after six cycles of mass selection for yield improvement and BS13 is a synthetic population developed from seven cycles of half-sib testing in BSSS followed by two cycles of S_1 progeny testing. All materials evaluated are listed in Table 3.

The Iowa reciprocal recurrent selection program was initiated in 1949 with BSSS and BSCB1 used as the source

Table 2. Inbred lines that were combined to form BSSS and BS B1 synthetic varieties

Synthetic population	
BSSS	BSCB1
AH83	A346
A36-3-1-3	CC5
F_1B-1-7-1	Hy
Hy	I205
I159	K230
I224A2	L317
LE23-1-6-2	Oh07
P3168	Oh33
Os420	Oh40B
TR9-1-16	Oh51A
12E	P8
2XWD456A	R4
187-2	
416-5	
540	
617-3-4	

Table 3. Listing of genetic materials and their respective entry numbers

Genetic material	Entry number
BSSS(R)C_0	1
BSSS(R)C_1	2
BSSS(R)C_3	3
BSSS(R)C_5	4
BSSS(R)C_7	5
BSCB1(R)C_0	6
BSCB1(R)C_1	7
BSCB1(R)C_3	8
BSCB1(R)C_5	9
BSCB1(R)C_7	10
BSSS(R)C_0 x BSCB1(R)C_0	11
BSSS(M)C_6	12
BS13	13
BSSS(R)C_5 x BSCB1(R)C_5	14
BSSS(R)C_7 x BSCB1(R)C_7	15

populations. To start the program a large number of S_0 plants in the original (C_0) populations was self-pollinated and used as male parent to cross with about 10 randomly chosen plants in the opposite population. At harvest the ears with the same male parent were bulked to form one testcross entry.

Approximately 100 testcrosses were harvested from each population. The selfed seed was harvested and put in cold storage. The two sets of testcrosses were evaluated the following year in separate experiments. Data from the yield trials were used as the main criterion for selecting superior S_1 lines, but some attention was also given to lodging resistance and moisture percent of the grain at harvest. The selfed seeds from the 10 selected lines were grown ear-to-row for each population, and all possible (45) intercrosses were made among them. Four to six plant by plant crosses were made between each pair of lines and the seed from each pair of rows was bulk harvested and kept separate from the others. Equal quantities of seed from each of the 45 S_1 progeny single-crosses were bulked for each population. Each population was grown in isolation the following year. The reason for this was to allow each population to random mate and enhance recombinations.

The procedures described above remained much the same for the first five cycles of selection. However, the season of random mating after intercrossing the selected lines was discontinued after the first cycle. The reasons were twofold; one cycle of selection could be completed in three instead of four years, and pedigrees could be maintained on the selected lines. In the cycles following the first the 45 single-crosses were kept separate for each population. To initiate a new cycle two plants from each of the 45 single crosses were selfed and crossed to the opposite population.

This made 90 selfs and testcrosses in each population. A third plant was chosen from some single-crosses to bring the total number of selfs and testcrosses to approximately 100 in both populations. S_1 lines to be recombined were selected mainly on their testcross performance, but some consideration also was given to the pedigree of the line. In some cases a lower yielding (although not significantly) line was selected instead of a higher yielding line whose pedigree showed it to be related to the others in the selected group. This was done to minimize inbreeding in the populations.

At the start of the sixth cycle (C5) some major changes were initiated. One change was to self a large number of S_0 plants in each population prior to forming the testcrosses. With this modification S_1 plants were used as pollen parents, and S_2 lines were recombined to form the improved synthetics. A plant from each of the S_1 lines was self-pollinated and crossed to several random S_0 plants from the other population. More than one self and testcross may have been formed within an S_1 line but only one was saved at harvest. While the testcrosses were being formed the S_1 lines also were being evaluated for European corn borer resistance and stalk rot (Diplodia zea, Pass) resistance in separate breeding nurseries. Some S_1 lines were eliminated before pollination because of high European corn borer feeding scores, and more were eliminated at harvest due to poor stalk rot ratings. Ample S_1 lines were planted to ensure about 100 selfs and

testcrosses remained in each population after the European corn borer and stalk rot selections had been made. The S_1 plants were selfed and the intercrosses among the selected S_2 lines were made in winter nurseries; thus, one cycle was completed in three years.

The number of testcrosses deviated slightly from cycle to cycle but was approximately 100 in all cycles. The number of environments and replications used in the testcross yield trials has varied with cycles of selection also. The number of environments, replications used in each environment, and testcrosses evaluated in each cycle is summarized in Table 4.

Plot techniques and agronomic practices employed in the yield trials have changed over cycles to keep pace with the current production practices. The yield trials were hand harvested and dropped ears were gleaned from the plots. Since the fifth cycle the plots have been machine harvested, and the dropped ears have not been picked up. Plant densities in the yield trials have increased from about 29,000 plants per hectare in the first cycle to approximately 51,000 plants per hectare in the latest cycles. No exact record of fertilizer application rates is available, but soil fertility levels on the experimental plot areas have generally increased over time.

Mass selection techniques used in BSSS were patterned after those described by Gardner (1961). In each cycle of selection the most recent version of the population was grown

Table 4. Summary of number of yield trials, replications per trial, and number of testcrosses in the selection populations from the reciprocal recurrent selection program

Selection population	Number of trials	Replications per trial	Number of testcrosses
BSSS(R)C_0	1	3	100
BSSS(R)C_1	2	3	103
BSSS(R)C_2	4	27[a]	103
BSSS(R)C_3	2	3	103
BSSS(R)C_4	4	2	103
BSSS(R)C_5	4	2	100
BSSS(R)C_6	3	2	100
BSSS(R)C_7	3	2	100
BSCB1(R)C_0	1	3	100
BSCB1(R)C_1	2	3	103
BSCB1(R)C_2	4	3	103
BSCB1(R)C_3	2	3	103
BSCB1(R)C_4	4	2	90
BSCB1(R)C_5	4	2	100
BSCB1(R)C_6	3	2	100
BSCB1(R)C_7	3	2	100

[a]Harmonic mean.

in isolation. About 0.4 hectare was subdivided into approximately 100 rectangular grids. Each grid contained 40 competitive plants. At harvest 8 to 12 ears of the highest yielding plants were phenotypically selected from each grid unit. The ears were then dried, shelled, and weighed. Equal quantities of seed from the three highest yielding plants from each grid

were bulked to provide seed for the next cycle of selection. Since 3 of 40 plants were selected, selection intensity was 7.5% per cycle. Selection was conducted in a single environment at Ames, Iowa, for all cycles at plant densities of about 39,000 plants per hectare.

BS13 is an improved synthetic developed following seven cycles of half-sib selection with the double-cross Iowa 13 as tester and two cycles of S_1 selection. In the half-sib selection program S_0 plants were used as pollen parents and S_1 lines were recombined to form the new population. Ten S_1 lines were recombined and approximately 100 testcrosses were evaluated in each cycle. In the S_1 selection cycles S_0 plants were selfed, and the resulting S_1 lines were grown ear-to-row. The 10 highest yielding S_1 lines were recombined using remnant seed.

Seed for the C_0xC_0, C_5xC_5, and C_7xC_7 population crosses was prepared by planting the populations side by side in paired rows. There were five such pairs of rows with each row having 25 plants for each CnxCn cross. An attempt was made to pollinate all ears in each row. Plants were not used as pollen parents more than twice. Seed for the C_0, C_1, C_3, C_5, and C_7 populations themselves and the BS13 entry was prepared by planting six paired rows each with 25 plants of the given entry and sib-mating the plants within the row. Again each ear in a row was pollinated, and a plant served as male parent no more than twice. Seed for the BSSS(M)C_6 entry was

obtained as a sample of the syn-3 generation of the BSSS(M)C_6 population. The seed for all entries was produced in 1974.

Field Procedures

This experiment was grown at the Agronomy and Agricultural Engineering Research Center and at the Hinds farm near Ames and at Ankeny in 1975 and 1976. The experimental design was a randomized complete block with 15 entries and five replications in each environment. A plot consisted of two rows 518.2 cm long and either 76.2 cm or 101.6 cm between rows. Blocks were bordered by a single-cross filler hybrid. All plots were hand planted to 17 two-plant hills per row and later thinned to one plant per hill. Pertinent information relative to the experimental environments is given in Table 5.

All plots were hand harvested, and dropped ears were picked up. Ears were then artificially dried to constant moisture. After drying, ear length, ear diameter, and cob diameter were measured in centimeters from a sample of 20 ears from each plot. Kernel depth was calculated by subtracting cob diameter from ear diameter. Grain yield was taken as weight in grams of shelled grain from all ears in a plot and later converted to quintals per hectare. Weight of 300 kernels was measured to the nearest decigram from a sample of grain from each plot. Ears per plant was obtained by dividing number of ears per plot by the number of plants per plot. Plant height was measured to the nearest centimeter

Table 5. Information relative to the six experimental environments

Environment	Year of evaluation	Location	Plot length (cm)	Row width (cm)	Plant spacing (cm)	Stand density (plants/ha)
1	1975	Ames, Research Center	518.2	101.6	30.5	32,291
2	1975	Ames, Hinds Farm	518.2	101.6	30.5	32.291
3	1975	Ankeny	518.2	76.2	30.5	43,054
4	1976	Ames, Research Center	518.2	76.2	30.5	43,054
5	1976	Ames, Hinds Farm	518.2	76.2	30.5	43,054
6	1976	Ankeny	518.2	76.2	30.5	43,054

as the distance between the ground and the flag leaf collar. Ear height was measured to the nearest centimeter as the distance between the ground and the top ear node. Ear height was subtracted from plant height to obtain top height. The plant characteristics were measured on 20 competitive plants in a plot. Date of 50% silk was recorded as the number of days from July 1, until 50% of the plants had emerged silks. Date of 50% silk was measured only at the Research Center in 1975 and 1976. All other traits were measured in all six environments.

Analysis of Field Data

Analysis of variance and regression analysis

The data collected on each trait were first analyzed on a plot mean basis for each environment. The plot means were analyzed using the following model:

$$Y_{ij} = u + R_i + V_j + e_{ij} \quad ,$$

where

Y_{ij} = observed value in the ij^{th} plot,

u = overall mean,

R_i = effect of the i^{th} replication ($i=1...5$),

V_j = effect of the j^{th} entry ($j=1....15$), and

e_{ij} = error associated with the ij^{th} observation.

The analysis of variance table computed from this model is shown in Table 6.

Table 6. Analysis of variance for a given trait in one environment

Source	d.f.	E(MS)
Replications	(r-1)	$\sigma^2 + v\sigma^2_R$
Entries	(v-1)	$\sigma^2 + rK^2_V$
Error	(r-1)(v-1)	σ^2

The analysis was then combined over environments according to the following model:

$$Y_{ijk} = u + E_i + R_{ij} + V_k + (VE)_{ik} + e_{ijk} \quad ,$$

where

Y_{ijk} = observed value of the ijk^{th} plot,

u = overall mean,

E_i = effect of the i^{th} environment (i=1...6),

R_{ij} = effect of the j^{th} replication within the ith environment (j=1...5),

V_k = effect of the k^{th} entry (k=1...15),

$(VE)_{ik}$ = effect of interaction between the k^{th} entry and the i^{th} environment, and

e_{ijk} = error associated with the ijk^{th} observation.

Table 7 shows the analysis of variance table obtained from this model. Yield data were adjusted for stand differences by using covariance analysis in the individual and combined analyses. Each location-year combination was considered as

Table 7. Analysis of variance for a given trait combined over environments

Source	d.f.	E(MS)
Environments (env)	e-1	$\sigma^2 + v\sigma^2_{R/E} + rv\sigma^2_E$
Replications/env	(r-1)e	$\sigma^2 + v\sigma^2_{R/E}$
Entries (ent)	(v-1)	$\sigma^2 + r\sigma^2_{ExV} + reK^2_V$
Env x ent	(e-1)(v-1)	$\sigma^2 + r\sigma^2_{ExV}$
Pooled error	e(r-1)(v-1)	σ^2

an environment. Environments were treated as random and entries were treated as fixed effects in all analyses.

Regression procedures were used to partition the entries sums of squares to assess progress in the populations themselves and the population crosses developed by reciprocal recurrent selection. Estimates of regression coefficients for both populations and the population cross were obtained from two models (linear and quadratic) to determine change over cycles of selection for each trait. The two regression models were fitted to the entry means in each environment and then combined over environments. The linear regression model was:

$$Y_{ij} = u + b_1 C_j + e_{ij} \quad ,$$

where

Y_{ij} = observed entry mean of the i^{th} population or population cross in the j^{th} cycle of selection,

u = overall mean,

b_1 = linear regression coefficient,

C_j = j^{th} cycle of selection, and

e_{ij} = deviation from regression.

A quadratic model was also fitted to the data. The quadratic coefficients were obtained by squaring the linear coefficients. The quadratic model was:

$$Y_{ij} = u + b_1 C_j + b_2 C_j^2 + e_{ij} \quad ,$$

where

Y_{ij} = observed entry mean of the i^{th} population or population cross in the j^{th} cycle of selection,

u = overall mean,

b_1 = linear regression coefficient,

C_j = j^{th} cycle of selection,

b_2 = quadratic regression coefficient,

C_j^2 = j^{th} cycle of selection squared, and

e_{ij} = deviation from regression.

The linear, quadratic, and deviation sums of squares for both populations and the linear and deviation sums of squares for the population cross were calculated by fitting the above model. This made it possible to check these mean squares for significance. The form of the analysis combined over environ-

ments produced from this model is shown in Table 8. Since the regression models were fitted to entry means, all sums of squares were multiplied by five (the number of replications) to make them comparable with the pooled error which was obtained from the original combined analysis. The pooled error was used to make tests of significance for the mean squares of the entries in the combined analyses except when the environments x entries mean square was significant. In those situations the environment x entries mean square was used to make tests of significance for the entries.

The combined analysis was partitioned in yet another way to assess the stability of entries over environments (Eberhart and Russell, 1966). The following model was used:

$$Y_{ij} = u_i + b_i I_j + \gamma_{ij} \quad ,$$

where

Y_{ij} = entry mean of the i^{th} entry in the j^{th} environment ($i=1...15$, $j=1...6$),

b_i = regression coefficient that measures the response of the i^{th} entry to varying environments,

γ_{ij} = deviation from regression of the i^{th} entry at the j^{th} environment,

I_j = environmental index obtained as the mean of all entries at the j^{th} environment minus the grand mean, and

u_i = mean of the i^{th} entry over all environments.

The appropriate analysis of variance table is given in Table 9.

Table 8. Analysis of variance combined over environments for a given trait with main effects partitioned

Source	d.f.		E(MS)
Environments (env)	(e-1)		$\sigma^2 + v\sigma^2_{R/E} + rv\sigma^2_E$
Replications/env	e(r-1)		$\sigma^2 + v\sigma^2_{R/E}$
Entries (ent)	(v-1)		$\sigma^2 + r\sigma^2_{ExV} + reK^2_V$
BSSS(R)		(a-1)	$\sigma^2 + r\sigma^2_{ExA} + reK^2_A$
Linear (L)		1	$\sigma^2 + r\sigma^2_{ExL} + reK^2_L$
Quadratic (Q)		1	$\sigma^2 + r\sigma^2_{ExQ} + reK^2_Q$
Deviations (D)		2	$\sigma^2 + r\sigma^2_{ExD} + reK^2_D$
BSCBl(R)		(b-1)	$\sigma^2 + r\sigma^2_{ExB} + reK^2_B$
L		1	$\sigma^2 + r\sigma^2_{ExL} + reK^2_L$
Q		1	$\sigma^2 + r\sigma^2_{ExQ} + reK^2_Q$
D		2	$\sigma^2 + r\sigma^2_{ExD} + reK^2_D$
BSSS(R) x BSCBl(R)		(c-1)	$\sigma^2 + r\sigma^2_{ExC} + reK^2_C$
L		1	$\sigma^2 + r\sigma^2_{ExL} + reK^2_L$
D		1	$\sigma^2 + r\sigma^2_{ExD} + reK^2_D$
Residual (res)	4		
Env x ent	(e-1)(v-1)		$\sigma^2 + r\sigma^2_{ExV}$

Table 8. (Continued)

Source	d.f.	E(MS)
Env x BSSS(R)	(e-1)(a-1)	$\sigma^2 + r\sigma^2_{ExA}$
Env x L	(e-1)	$\sigma^2 + r\sigma^2_{ExL}$
Env x Q	(e-1)	$\sigma^2 + r\sigma^2_{ExQ}$
Env x D	(e-1)2	$\sigma^2 + r\sigma^2_{ExD}$
Env x BSCB1(R)	(e-1)(b-1)	$\sigma^2 + r\sigma^2_{ExB}$
Env x L	(e-1)	$\sigma^2 + r\sigma^2_{ExL}$
Env x Q	(e-1)	$\sigma^2 + r\sigma^2_{ExQ}$
Env x D	(e-1)a	$\sigma^2 + r\sigma^2_{ExD}$
Env x BSSS(R) x BSCB1(R)	(e-1)(c-1)	$\sigma^2 + r\sigma^2_{ExC}$
Env x L	(e-1)	$\sigma^2 + r\sigma^2_{ExL}$
Env x D	(e-1)	$\sigma^2 + r\sigma^2_{ExD}$
Env x res	$(e-1)^4$	
Pooled error	e(r-1)(v-1)	σ^2

Table 9. Analysis of variance when stability parameters are estimated

Source	d.f.	MS
Environments (linear) (env_1)	1	
Replications/env	e(r-1)	
Entries	(v-1)	MS_1
Env_1 x entries	(v-1)	MS_2
Deviations (pooled)	v(e-2)	MS_3
Entry 1	e-2	
.		
.		
.		
.		
Entry 15	e-2	
Pooled error	e(r-1)(v-1)	

$MS_2/MS_3 = F$ was used as an approximate F-test to test the hypothesis of no difference among entries for their regression on the environmental index. Deviations from regression for each entry were tested using the pooled error mean square. Tests between individual regression coefficients were made using the appropriate t-test.

Expected progress from selection

Expected gains from reciprocal recurrent and mass selection were calculated using estimates of variance components. Gain from reciprocal recurrent selection was calculated as:

$$\Delta G = \frac{K\frac{1}{4}\sigma^2_{A(1)}}{\sqrt{\frac{\sigma^2_{e(1)}}{rm} + \frac{\frac{1}{4}\sigma^2_{AE(1)}}{m} + \frac{1}{4}\sigma^2_{A(1)}}} + \frac{K\frac{1}{4}\sigma^2_{A(2)}}{\sqrt{\frac{\sigma^2_{e(2)}}{rm} + \frac{\frac{1}{4}\sigma^2_{AE(2)}}{m} + \frac{1}{4}\sigma^2_{A(2)}}},$$

where

ΔG = expected gain from one cycle of selection,

K = standardized selection differential,

$\sigma^2_{A(1)}$ and $\sigma^2_{A(2)}$ = genetic variance among half-sib families for populations 1 and 2 when the opposite population is used as the tester,

$\sigma^2_{AE(1)}$ and $\sigma^2_{AE(2)}$ = variance due to interaction of genotypes (half-sib families) with environments in populations 1 and 2, respectively,

$\sigma^2_{e(1)}$ and $\sigma^2_{e(2)}$ = experimental error variances associated with testcrosses from populations 1 and 2, respectively,

m = number of environments, and

r = number of replications in each environment.

Gain per cycle from mass selection was computed as:

$$\Delta G = \frac{K\frac{1}{2}\sigma^2_A}{\sqrt{\sigma^2_w + \sigma^2_{AE} + \sigma^2_{DE} + \sigma^2_A + \sigma^2_D}}$$

where

K = standardized selection differential,

σ^2_A = additive genetic variance in the population,

σ^2_D = dominance variance in the population,

σ^2_w = within plot variance,

σ^2_{AE} = variance due to interaction of additive variance with environments, and

σ^2_{DE} = variance due to interaction of dominance variance with environments.

Estimation of inbreeding

Ten lines were recombined to form the new version of the BSSS(R) and BSCB1(R) populations in all selection cycles. Inbreeding coefficients in the populations were estimated using the formula from Falconer (1960);

$$F_t = \frac{1}{2N+1} + (1 - \frac{1}{2N+1}) F_{t-1} \quad ,$$

where

F_t = inbreeding coefficient in the t^{th} generation and

N = effective population size.

Computer Simulation

A computer program was written to simulate as nearly as possible reciprocal recurrent selection as it is done under field conditions with maize. Much of the logic used in the simulation program was adapted from Fraser and Burnell (1970).

Digital computers store and process information using vectors of binary digits. Binary digits can be used to represent genetic situations. For example, the genotype A/a can be represented as 1/0 in the computer. Similarly, the multigenic

genotype, AbCd/ABcd, can be represented as 1010/1100. With the assumption of no linkage, the loci can be interpreted either as segregating independently from the same chromosome or arising from different chromosomes.

In the simulation study each individual consisted of 40 independently segregating loci, each with two alleles. The difference between the dominant and recessive homozygous genotypes was four at all loci. Therefore, the maximum attainable value for an individual was 160.

Six sets of starting conditions were obtained by imposing three levels of dominance and two different gene frequencies in the initial populations. The six starting conditions are itemized in Table 10.

The simulation of reciprocal recurrent selection can be subdivided into five steps. The steps are:

1. Generate the initial populations;
2. Form the testcrosses;
3. Evaluate the testcrosses;
4. Recombine the selected lines; and
5. Determine population parameters.

These five steps must be completed for both populations. Each step will be described in some detail.

1. Each population consisted of 110 individuals throughout all cycles of selection with each individual having 40 loci each with two alleles per locus. The initial populations were generated by placing a 0 or 1 at each allelic position

Table 10. Listing of starting conditions in the two populations used in the simulation study of reciprocal recurrent selection

Condition	Level of dominance	Frequency of favorable allele in population	
		A	B
1	1.00	0.50	0.50
2	0.75	0.50	0.50
3	0.00	0.50	0.50
4	1.00	0.25	0.50
5	0.75	0.25	0.50
6	0.00	0.25	0.50

with a probability depending on the selected gene frequency. This was accomplished by comparing the uniform random variate $0 \leq X \leq 1$ with the selected frequency to determine if a 0 or 1 should be placed in that allelic position. The uniform random variates were generated using subroutine GGUB from the IMSL Subroutine Library. Considering the 110 individuals in each population, the 40 loci had the same starting frequency except for chance fluctuations.

2. One hundred and ten testcrosses were formed for each population in all selection cycles. Each testcross was formed by mating one male to four random females in the opposite population, and each mating produced one progeny. Before forming the testcrosses each male was selfed one generation.

The same selfed (S_1) individual was mated to the four females, but a different male gamete was produced for each mating.

Random gametes were produced from the parents by performing a random walk along the 40 loci. The selection of successive alleles for the gamete was made by comparing the random uniform variate $0 \leq X \leq 1$ with the recombination value r, which is 0.5 for independent assortment. Consider the parental genotype, 1010/1100, and the sequence of random numbers 0.72, 0.16, 0.54, and 0.37. The gamete produced would be 1000. The genotypic value of each progeny was determined by multiplying the number of favorable alleles by half the difference between the two homozygous genotypes (2 in this case) and adding the product of the number of heterozygous loci times the level of dominance.

3. The testcrosses were evaluated on the basis of half-sib family means. Genotypic mean values were calculated by averaging the individual progeny values. A phenotypic mean value for each testcross was obtained by adding a deviate to the genotypic mean value. The deviates were chosen to be independent, normally distributed with mean zero and variance 100. The random normal variates were generated using subroutine GGNOR from the IMSL Subroutine Library. Genotypic and phenotypic variances among half-sib families were calculated using the genotypic and phenotypic values, respectively. The 11 superior genotypes were selected to be recombined on the basis of phenotypic values.

4. The new populations were produced by making the 55 possible single-crosses among the 11 selected lines. Two progeny were produced from each mating to maintain the population size at 110 in all cycles. All individuals were selfed one generation before crossing; therefore, S_2 lines were recombined. The same S_1 individual was used to represent a given line, but a different S_2 was used in each mating.

5. The mean of the populations themselves was calculated by averaging the 110 genotypic values in each population. The mean of the population cross was calculated as the mean genotypic value of the testcrosses. The frequency of the favorable allele was calculated for each of the 40 loci in all selection cycles. Finally, these individual frequencies were used to calculate average frequencies in the populations.

Ten cycles of reciprocal recurrent selection were simulated, and duplicate runs were made for each starting condition. The simulation program was written in PL/1. A source listing of the program statements is found in Appendix B.

Analysis of simulated data

Linear and quadratic regression models were fitted to the simulated data to assess the response to selection over the 10 cycles. The following linear model was used:

$$Y_{ij} = u + b_1 C_j + e_{ij} \quad ,$$

where

Y_{ij} = observed mean of the i^{th} population or population

cross in the j^{th} cycle of selection,

u = overall mean,

b_1 = linear regression coefficient,

C_j = j^{th} cycle of selection, and

e_{ij} = deviation from regression.

The quadratic model was:

$$Y_{ij} = u + b_1 C_j + b_2 C_j^2 + e_{ij} \quad ,$$

where

Y_{ij} = observed mean of the i^{th} population or population cross in the j^{th} cycle of selection,

u = overall mean,

b_1 = linear regression coefficient,

C_j = j^{th} cycle of selection,

b_2 = quadratic regression coefficient,

C_j^2 = j^{th} cycle of selection squared, and

e_{ij} = deviation from regression.

The two regression models were fitted to the simulated data for each duplicate run and starting condition.

Expected gain from selection was calculated using variance components obtained from the testcrosses as:

$$\Delta G = \frac{K\sigma^2_{G_A}}{\sqrt{\frac{\sigma^2_{e_A}}{4} + \sigma^2_{G_A}}} + \frac{K\sigma^2_{G_B}}{\sqrt{\frac{\sigma^2_{e_B}}{4} + \sigma^2_{G_B}}} \quad ,$$

where

ΔG = gain from one cycle of selection,

K = standardized selection differential,

$\sigma^2_{G_A}$ and $\sigma^2_{G_B}$ = genotypic variance among testcrosses in populations A and B, respectively, and

σ^2_{EA} and σ^2_{EB} = environmental variance associated with testcrosses in populations A and B, respectively.

The variance components used in the prediction equation were the means of the two duplicate runs.

The simulated selection populations were treated as 33 entries and further analyzed using the following model:

$$Y_{ij} = u + r_i + v_j + e_{ij}$$

where

Y_{ij} = observed value of the j^{th} simulated entry in the i^{th} replicate (i=1,2), (j=1...33),

u = overall mean,

r_i = effect of the i^{th} replicate,

v_j = effect of the j^{th} entry, and

e_{ij} = error associated with the ij^{th} observation.

The analysis of variance produced from this model is shown in Table 11. The errors from these analyses of variance were used to calculate standard errors for the selection populations for the appropriate starting condition.

Table 11. Form of analysis of variance for genotypic means and mean frequency of favorable allele in the simulated selection population

Source	d.f.	E(MS)
Replicates	r-1	$\sigma^2 + e\sigma_R^2$
Entries	e-1	$\sigma^2 + rK_E^2$
Error	(r-1)(e-1)	σ^2

RESULTS AND DISCUSSION

Mean values and coefficients of variation (C.V.) for all traits in individual environments are presented in Table 12. The C.V. percentages are acceptable for maize experiments of this type. Changes in C.V. values within a trait can be attributed mainly to changes in means rather than changes in experimental error across environments.

All environments suffered some moisture stress during July and August. Yield reductions were most severe in environments 2 and 5. Hail partially defoliated the plants in environment 4 before tasseling.

Stability Analysis

The conventional analysis of variance for grain yield is shown in Table 13. Highly significant mean squares ($P < .01$) were observed for environments, entries, and environments x entries. The stability analysis (Table 14) partitions the environment x entry sums of squares for each entry into two parts: (1) variation due to differing responses of the entry to varying environmental indexes (sums of squares due to regression), and (2) sums of squares not accounted for by regression (deviations from regression). The environment (linear) x entries sums of squares is significant ($P < .05$) indicating entries responded differently to the varying environmental indexes. Similarly, the pooled deviations from

Table 12. Mean and coefficient of variation (C.V.,%) for each trait in each environment)

	Environment					
	1		2		3	
Trait	Mean	C.V.	Mean	C.V.	Mean	C.V.
Yield (q/ha)	64.0	9.35	46.5	12.35	69.1	12.99
Date silk [a]	20.6	4.36				
Plant height (cm)	213.9	3.73	194.7	3.95	182.7	5.61
Ear height (cm)	109.8	4.69	93.6	5.39	91.3	9.26
Top height (cm)	104.2	5.18	101.0	4.90	91.4	6.46
Ear length (cm)	19.0	5.08	18.6	4.98	18.8	5.42
Ear diameter (cm)	4.7	2.21	4.7	2.75	4.7	3.54
Cob diameter (cm)	2.9	3.03	2.9	2.44	2.9	3.57
Kernel depth (cm)	1.8	6.30	1.7	6.99	1.8	8.65
Ears/plant	1.22	8.21	1.03	8.38	0.99	5.74
300-kernel weight (g)	79.2	5.71	76.8	5.54	84.2	5.40

[a]Days after July 1.

Table 12. (Continued)

	Environment					
	4		5		6	
Trait	Mean	C.V.	Mean	C.V.	Mean	C.V.
Yield (q/ha)	51.2	7.93	25.4	24.36	71.4	7.63
Date silk	25.4	7.76				
Plant height (cm)	184.9	2.75	192.7	2.88	213.5	2.88
Ear height (cm)	82.1	4.63	86.2	4.10	100.5	4.67
Top height (cm)	102.8	4.41	106.4	4.03	113.0	3.44
Ear length (cm)	17.2	11.26	15.3	7.09	18.8	4.28
Ear diameter (cm)	4.4	3.19	3.9	5.79	4.7	2.05
Cob diameter	2.7	2.85	2.6	4.29	2.8	4.17
Kernel depth (cm)	1.7	9.51	1.4	14.89	1.8	6.89
Ears/plant	1.60	8.18	0.79	13.71	1.04	7.11
300 kernel weight (g)	69.3	8.90	66.6	9.51	78.3	5.64

Table 13. Analysis of variance for grain yield (q/ha) for the 15 entries combined over five environments

Source	d.f.	Mean squares
Environments (env)	5	22679.72**
Replications/env)	24	163.50**
Entries	14	1268.90**
Env x entries	70	107.20**
Pooled error	330	38.99

**Significant at the 0.01 level.

Table 14. Stability analysis for grain yield (q/ha) for the 15 entries

Source	d.f.	Mean squares
Environments linear (env_1)	1	113398.31**
Replications/env_1	24	163.50**
Entries	14	1268.90**
Env_1 x entries	14	182.32*
Deviations (pooled)	60	82.53**
Pooled error	330	38.99

*,**Significant at the 0.05 and 0.01 level, respectively.

regression is significant ($P < .01$).

Regression coefficients (b_1), deviations from regression (S_d^2), and coefficients of determination (R^2) for individual entries are presented in Table 15. R^2 values have been included with the S_d^2 values because R^2 values are easy to interpret and are independent of measurement units. When individual b_1 values were tested with the appropriate t-test, only the BSSS(R)C_3, BSCB1(R)C_3, BSCB1(R)C_7, BSS(R)C_5x BSCB1(R)C_5, and BSSS(R)C_7xBSCB1(R)C_7 entries had b_1 values different from 1.0 ($P < .05$). There is a trend for the b_1 values in the selection populations themselves to decline and b_1 values for the population crosses to increase over selection cycles. The trends, however, are not significant ($P < .05$); that is, b_1 values for BSSS(R)C_0 and BSSS(R)C_7, BSCB1(R)C_0 and BSCB1(R)C_7, and BSSS(R)C_0xBSCB1(R)C_0 and BSSS(R)C_7xBSCB1(R)C_7 are not different when tested with the appropriate t-test. The only S_d^2's showing significance were BSSS(M)C_6 ($P < .01$) and BSSS(R)C_1 ($P < .05$).

Environmental indexes (mean yield in each environment expressed as a deviation from the overall mean) ranged from -29.2 to 16.9 with a reasonable distribution of values between the extremes. Eberhart and Russell (1966) stated the regression coefficients could be estimated from only a few environments provided they covered the range of expected responses, but several environments are needed to obtain a reliable estimate of deviations from regression. The six

Table 15. Regression coefficients (b), deviations from regression (S_d^2), and coefficients of determination (R^2) for the 15 entries from the stability analysis

Entry	b_1	S_d^2	R^2
BSSS(R)C_0	1.12 ± 0.095	67.75	0.97
BSSS(R)C_1	0.84 ± 0.122	111.93*	0.92
BSSS(R)C_3	0.86 ± 0.058	25.57	0.98
BSSS(R)C_5	1.10 ± 0.107	86.74	0.96
BSSS(R)C_7	0.92 ± 0.081	49.13	0.97
BSCBl(R)C_0	1.02 ± 0.096	70.57	0.97
BSCBl(R)C_1	0.97 ± 0.111	93.26	0.95
BSCBl(R)C_3	0.79 ± 0.078	45.96	0.96
BSCBl(R)C_5	0.90 ± 0.076	44.06	0.97
BSCBl(R)C_7	0.77 ± 0.045	15.07	0.99
BSSS(R)C_0xBSCBl(R)C_0	1.13 ± 0.075	42.53	0.98
BS13	1.03 ± 0.087	56.83	0.97
BSSS(M)C_6	1.02 ± 0.240	434.59**	0.82
BSSS(R)C_5xBSCBl(R)C_5	1.29 ± 0.07	37.27	0.99
BSSS(R)C_7xBSCBl(R)C_7	1.22 ± 0.086	56.75	0.98

*,**Significant at the 0.05 and 0.01 levels, respectively.

environments in this study provided a broad range of responses. The number of environments in this study may be minimal to accurately estimate the S_d^2 values.

Eberhart and Russell (1966) defined a stable genotype to be one with $b_1 = 1.0$, $S_d^2 = 0$, and a high mean. Finlay and Wilkinson (1963) stated a genotype with a $b_1 < 1.0$ was stable and adapted to low yielding environments. Bilbro and Ray (1976) further suggested the b_1 values should be used as indicators of a genotype's stability and S_d^2 and/or R^2 values should be used as measures of stability. Eberhart and Russell's (1966) definition of stability will be used here.

Perhaps the most striking result of the stability analysis is the large S_d^2 associated with the BSSS(M)C_6 entry. This mean square is four times larger than any other deviation mean square. All other deviation mean squares are of similar magnitude. With mass selection genotypes are evaluated in only one environment whereas genotypes are evaluated in several environments with the other selection methods. The selection of genotypes in a specific environment has produced a selection population that is less predictable under varying environments than the original population.

Fakorede (1977) evaluated the same C_0xC_0, C_5xC_5, and C_7xC_7 population crosses of BSSS(R) and BSCB1(R) at four nitrogen levels and four plant densities in each of three environments. Stability analyses were performed on different nitrogen, density, and environment combinations. The improved

population crosses gave a greater response to higher nitrogen levels; that is, the improved population crosses had greater b_1 values. Similarly, the improved population crosses had less yield reduction at high plant densities. S_d^2 values were generally not significant.

Observed Response from Selection

The relationship between traits measured and cycles of selection was investigated by using regression analysis. Linear and quadratic regression models were fitted to the data for the populations themselves and the population crosses. The combined analysis of variance tables with main effects partitioned for each trait are presented in Tables 16 to 26. Highly significant ($P < .01$) entry and environment effects were found for all traits measured. There was no significant interaction ($P < .05$) of entries with environments for days to 50% silk and 300-kernel weight. Environment x entries mean squares were significant at the 5% level for kernel depth and ear length, and all other traits showed significant interactions at the 1% level. In all instances, the entries accounted for much more of the variation than the entries x environment. Most of the environment x entries variation was accounted for by the environment x residual source.

Both a linear and quadratic model were fitted to the combined entry means. When expressed as a percentage of the entries sums of squares, the linear model accounted for most

Table 16. Analysis of variance for the 15 entries combined over five environments with main effects partitioned to show the effects of cycles of selection on grain yield (q/ha)

Source	d.f.	Mean squares	F-ratio
Environment (env)	5	22679.72	138.71**
Replications/env	24	163.50	4.19**
Entries (ent)	14	1268.90	11.84**
BSSS(R)Cn	4	157.56	1.47ns[a]
Linear (lin)	1	368.20	3.43ns
Quadratic (quad)	1	68.12	0.64ns
Deviations (dev)	2	96.97	0.90ns
BSCBl(R)Cn	4	140.50	1.31ns
Lin	1	324.38	3.03ns
Quad	1	185.00	1.73ns
Dev	2	26.25	0.25ns
BSSS(R)CnxBSCBl(R)Cn	2	1183.03	11.04**
Lin	1	2365.29	22.06**
Dev	1	0.76	0.01ns
Residual (res)	4	3551.58	33.13*
Env x ent	70	107.20	2.75**
Env x BSSS(R)Cn	20	84.22	2.16**
Env x lin	5	25.87	0.66ns
Env x quad	5	56.50	1.45ns
Env x dev	10	127.25	3.26**
Env x BSCBl(R)Cn	20	38.20	0.98ns
Env x lin	5	88.73	2.28*
Env x quad	5	19.64	0.50ns
Env x dev	10	22.23	0.57ns
Env x BSSS(R)CnxBSCBl(R)Cn	10	52.04	1.33ns
Env x lin	5	91.79	2.35*
Env x dev	5	12.55	0.32ns
Env x res	20	226.76	5.82**
Pooled error	(330) 336	38.99	

[a]ns = nonsignificant in this and all subsequent tables.

*,**Significant at the 0.05 and 0.01 level, respectively.

Table 17. Analysis of variance for the 15 entries combined over two environments with main effects partitioned to show the effects of cycles of selection on date of 50% silk emergence

Source	d.f.		Mean squares	F-ratio
Environments (env)	1		854.40	175.80**
Replications/env	8		4.86	2.08*
Entries (ent)	14		47.77	20.41**
BSSS(R)Cn		4	23.82	10.18**
Linear (lin)		1	33.61	14.36**
Quadratic (quad)		1	17.88	7.64**
Deviations (dev)		2	10.95	4.68*
BSCB1(R)Cn		4	17.53	7.49**
Lin		1	47.18	20.16**
Quad		1	17.35	7.41**
Dev		2	5.59	2.39ns
BSSS(R)CnxBSCB1(R)Cn		2	7.24	3.09ns
Lin		1	13.39	5.72*
Dev		1	1.08	0.46ns
Residual (res)		4	127.70	54.57**
Env x ent	14		4.11	1.76ns
Env x BSSS(R)Cn		4	3.12	1.33ns
Env x lin		1	2.50	1.07ns
Env x quad		1	3.06	1.31ns
Env x dev		2	3.47	1.48ns
Env x BSCB1(R)Cn		4	4.87	2.08ns
Env x lin		1	5.69	2.43ns
Env x quad		1	12.01	5.13*
Env x dev		2	1.78	0.76ns
Env x BSSS(R)CnxBSCB1(R)Cn		2	0.64	0.27ns
Env x lin		1	1.12	0.48ns
Env x dev		1	0.15	0.06ns
Env x res		4	5.97	2.55*
Pooled error	112		2.34	

*,**Significant at the 0.05 and 0.01 level, respectively.

Table 18. Analysis of variance for the 15 entries combined over five environments with main effects partitioned to show the effects of cycles of selection on plant height (cm)

Source	d.f.	Mean squares	F-ratio
Environment (env)	5	1432.02	5.21**
Replications/env	24	274.78	5.12**
Entries (ent)	14	4055.22	42.21**
BSSS(R)Cn	4	1197.93	12.44**
Linear (lin)	1	387.26	4.03*
Quadratic (quad)	1	1757.38	18.29**
Deviations (dev)	2	1317.54	13.71**
BSCB1(R)Cn	4	306.56	3.19*
Lin	1	843.79	8.78**
Quad	1	0.82	0.01ns
Dev	2	190.81	1.99ns
BSSS(R)CnxBSCB1(R)Cn	2	491.22	5.11**
Lin	1	946.00	9.85**
Dev	1	36.44	0.38ns
Residual (res)	4	12446.19	129.54**
Env x ent	70	96.08	1.79**
Env x BSSS(R)Cn	20	26.41	0.49ns
Env x lin	5	14.80	0.28ns
Env x quad	5	32.42	0.60ns
Env x dev	10	29.22	0.54ns
Env x BSCB1(R)Cn	20	66.78	1.24ns
Env x lin	5	45.50	0.85ns
Env x quad	5	56.86	1.06ns
Env x dev	10	82.39	1.53ns
Env x BSSS(R)CnxBSCB1(R)Cn	10	19.18	0.36ns
Env x lin	5	34.25	0.64ns
Env x dev	5	4.11	0.08ns
Env x res	20	233.50	4.35**
Pooled error	336	53.72	

*,**Significant at the 0.05 and 0.01 level, respectively.

Table 19. Analysis of variance for the 15 entires combined over five environments with main effects partitioned to show the effects of cycles of selection on ear height (cm)

Source	d.f.	Mean squares	F-ratio
Environment (env)	5	7506.11	54.40**
Replications/env	24	137.98	4.80**
Entries (ent)	14	8512.50	137.76**
BSSS(R)Cn	4	602.62	9.75**
Linear (lin)	1	1000.26	16.19**
Quadratic (quad)	1	992.81	16.07**
Deviations (dev)	2	208.71	3.38*
BSCB1(R)Cn	4	296.32	4.80**
Lin	1	932.49	15.09**
Quad	1	187.51	3.03ns
Dev	2	65.36	1.06ns
BSSS(R)CnxBSCB1(R)Cn	2	83.58	1.35ns
Lin	1	65.19	1.06ns
Dev	1	101.98	1.65ns
Residual (res)	4	9683.54	156.71**
Env x ent	70	61.79	2.15**
Env x BSSS(R)Cn	20	17.96	0.63ns
Env x lin	5	30.89	1.08ns
Env x quad	5	29.73	1.03ns
Env x dev	10	5.51	0.19ns
Env x BSCB1(R)Cn	20	34.60	1.20ns
Env x lin	5	38.17	1.33ns
Env x quad	5	24.45	0.85ns
Env x dev	10	37.88	1.32ns
Env x BSSS(R)CnxBSCB1(R)Cn	10	26.70	0.93ns
Env x lin	5	42.31	1.47ns
Env x dev	5	11.09	0.39ns
Env x res	20	150.42	5.24**
Pooled error	336	28.73	

*,**Significant at the 0.05 and 0.01 level, respectively.

Table 20. Analysis of variance for the 15 entries combined over five environments with main effects partitioned to show the effects of cycles of selection on top height (cm)

Source	d.f.	Mean squares	F-ratio
Environment (env)	5	3785.95	35.53**
Replications/env	24	106.57	4.49**
Entries (ent)	14	1041.62	22.93**
BSSS(R)Cn	4	930.90	20.49**
Linear (lin)	1	2616.28	57.59**
Quadratic (quad)	1	104.96	2.31ns
Deviations (dev)	2	501.17	11.03**
BSCB1(R)Cn	4	151.07	3.33*
Lin	1	2.62	0.06ns
Quad	1	216.70	4.77*
Dev	2	76.99	1.69ns
BSSS(R)CnxBSCB1(R)Cn	2	888.08	19.55**
Lin	1	1521.81	33.50**
Dev	1	254.36	5.60*
Residual (res)	4	2119.67	46.66**
Env x ent	70	45.43	1.91**
Env x BSSS(R)Cn	20	29.13	1.23ns
Env x lin	5	15.48	0.65ns
Env x quad	5	50.87	2.14ns
Env x dev	10	25.09	1.06ns
Env x BSCB1(R)Cn	20	38.22	1.61ns
Env x lin	5	33.92	1.43ns
Env x quad	5	60.38	2.54*
Env x dev	10	29.29	1.23ns
Env x BSSS(R)CnxBSCB1(R)Cn	10	25.99	1.09ns
Env x lin	5	41.81	1.76ns
Env x dev	5	10.17	0.43ns
Env x res	20	78.67	3.31**
Pooled error	336	23.74	

*,**Significant at the 0.05 and 0.01 level, respectively.

Table 21. Analysis of variance for the 15 entries combined over five environments with main effects partitioned to show the effects of cycles of selection on ear length (cm)

Source	d.f.	Mean squares	F-ratio
Environment (env)	5	159.75	48.56**
Replications/env	24	3.29	2.35**
Entries (ent)	14	29.33	15.20**
BSSS(R)Cn	4	7.26	3.76**
Linear (lin)	1	17.02	8.82**
Quadratic (quad)	1	0.01	0.01ns
Deviations (dev)	2	6.00	3.11*
BSCBl(R)Cn	4	12.66	6.65**
Lin	1	0.13	0.07ns
Quad	1	30.67	15.89**
Dev	2	9.92	5.14**
BSSS(R)CnxBSCBl(R)Cn	2	5.39	2.79ns
Lin	1	7.12	3.69ns
Dev	1	3.66	1.90ns
Residual	4	80.07	41.49**
Env x ent	70	1.93	1.38*
Env x BSSS(R)Cn	20	1.06	0.76ns
Env x lin	5	2.18	1.56ns
Env x quad	5	0.46	0.33ns
Env x dev	10	0.80	0.57ns
Env x BSCBl(R)Cn	20	1.93	1.38ns
Env x lin	5	3.02	2.16
Env x quad	5	1.36	0.97ns
Env x dev	10	1.67	1.19ns
Env x BSSS(R)CnxBSCBl(R)Cn	10	0.86	0.61ns
Env x lin	5	0.47	0.34ns
Env x dev	5	1.25	0.89ns
Env x res	20	3.34	2.39**
Pooled error	336	1.40	

*,**Significant at the 0.05 and 0.01 level, respectively.

Table 22. Analysis of variance for the 15 entries combined over five environments with main effects partitioned to show the effects of cycles of selection on ear diameter (cm)

Source	d.f.	Mean squares	F-ratio
Environment (env)	5	6.6396	68.95**
Replications/env	24	0.0963	4.26**
Entries (ent)	14	0.4939	11.33**
BSSS(R)Cn	4	0.0900	2.06ns
Linear (lin)	1	0.0527	1.21ns
Quadratic (quad)	1	0.1442	3.31ns
Deviations (dev)	2	0.0815	1.87ns
BSCB1(R)Cn	4	0.0942	2.16ns
Lin	1	0.3403	7.81**
Quad	1	0.0003	0.01ns
Dev	2	0.0180	0.41ns
BSSS(R)CnxBSCB1(R)Cn	2	0.0528	1.21ns
Lin	1	0.1038	2.38ns
Dev	1	0.0017	0.04ns
Residual (res)	4	1.5181	34.82**
Env x ent	70	0.0436	1.93**
Env x BSSS(R)Cn	20	0.0580	2.57ns
Env x lin	5	0.1375	6.08**
Env x quad	5	0.0378	1.67ns
Env x dev	10	0.0283	1.25ns
Env x BSCB1(R)Cn	20	0.0312	1.38ns
Env x lin	5	0.0360	1.59ns
Env x quad	5	0.0306	1.35ns
Env x dev	10	0.0290	1.38ns
Env x BSSS(R)CnxBSCB1(R)Cn	10	0.0328	1.47ns
Env x lin	5	0.0192	0.85ns
Env x dev	5	0.0463	2.05ns
Env x res	20	0.0471	2.08**
Pooled error	336	0.0226	

**Significant at 0.01 level.

Table 23. Analysis of variance for the 15 entries combined over five environments with main effects partitioned to show the effects of cycles of selection on cob diameter (cm)

Source	d.f.	Mean squares	F-ratio
Environment (env)	5	0.4698	14.82**
Replications/env	24	0.0317	2.41**
Entries (ent)	14	0.1303	5.74**
BSSS(R)Cn	4	0.0975	4.30**
Linear (lin)	1	0.0937	4.13**
Quadratic (quad)	1	0.0065	0.39ns
Deviations (dev)	2	0.1449	6.38**
BSCBl(R)Cn	4	0.0608	2.68*
Lin	1	0.0527	2.32ns
Quad	1	0.1821	8.02**
Dev	2	0.0042	0.19ns
BSSS(R)CnxBSCBl(R)Cn	2	0.0860	3.79*
Lin	1	0.0256	1.13ns
Dev	1	0.1463	6.44*
Residual (res)	4	0.2547	11.22**
Env x ent	70	0.0227	2.44**
Env x BSSS(R)Cn	20	0.0235	2.53**
Env x lin	5	0.0506	5.44**
Env x quad	5	0.0180	1.94ns
Env x dev	10	0.0127	1.37ns
Env x BSCBl(R)Cn	20	0.0238	2.56**
Env x lin	5	0.0422	4.54**
Env x quad	5	0.0185	1.99ns
Env x dev	10	0.0173	1.86*
Env x BSSS(R)CnxBSCBl(R)Cn	10	0.0161	1.73ns
Env x lin	5	0.0044	0.47ns
Env x dev	5	0.0278	2.99*
Env x res	20	0.0240	2.58**
Pooled error	336	0.0093	

*,**Significant at 0.05 and 0.01 level, respectively.

Table 24. Analysis of variance for the 15 entries combined over five environments with main effects partitioned to show the effects of cycles of selection on kernel depth (cm)

Source	d.f.	Mean squares	F-ratio
Environment (env)	5	2.4259	58.74**
Replications/env	24	0.0413	1.84*
Entries (ent)	14	0.3258	9.73**
BSSS(R)Cn	4	0.0733	2.19ns
Linear (lin)	1	0.1907	5.69*
Quadratic (quad)	1	0.0746	2.23ns
Deviation (dev)	2	0.0140	0.42ns
BSCB1(R)Cn	4	0.1017	3.04*
Lin	1	0.1880	5.61*
Quad	1	0.2095	6.25*
Dev	2	0.0046	0.14ns
BSSS(R)CnxBSCB1(R)Cn	2	0.1194	3.56*
Lin	1	0.0926	2.76ns
Dev	1	0.1463	4.37*
Residual (res)	4	0.9055	27.03**
Env x ent	70	0.0335	1.50*
Env x BSSS(R)Cn	20	0.0323	1.44ns
Env x lin	5	0.0410	1.85 ns
Env x quad	5	0.0089	0.40ns
Env x dev	10	0.0397	1.77ns
Env x BSCB1(R)Cn	20	0.0297	1.33ns
Env x lin	5	0.0152	0.68ns
Env x quad	5	0.1637	7.31**
Env x dev	10	0.0354	1.58ns
Env x BSSS(R)CnxBSCB1(R)Cn	10	0.0261	1.17ns
Env x lin	5	0.0234	1.04ns
Env x dev	5	0.0288	1.29ns
Env x res	20	0.0422	1.88*
Pooled error	336	0.0224	

*,**Significant at the 0.05 and 0.01 level, respectively.

Table 25. Analysis of variance for the 15 entries combined over five environments with main effects partitioned to show the effects of cycles of selection on number of ears per plant

Source	d.f.	Mean squares	F-ratio
Environment (env)	5	1.4075	49.56**
Replications/env	24	0.0284	3.79**
Entries (ent)	14	0.0951	5.28**
BSSS(R)Cn	4	0.0890	4.94**
Linear (lin)	1	0.2310	12.83**
Quadratic (quad)	1	0.0743	4.13*
Deviations (dev)	2	0.0253	1.41ns
BSCB1(R)Cn	4	0.0254	1.41ns
Lin	1	0.0811	4.51*
Quad	1	0.0179	0.99ns
Dev	2	0.0013	0.07ns
BSSS(R)CnxBSCB1(R)Cn	2	0.1361	7.50**
Lin	1	0.2207	12.26**
Dev	1	0.0515	2.86ns
Residual (res)	4	0.1503	8.35**
Env x ent	70	0.0180	2.40**
Env x BSSS(R)Cn	20	0.0118	1.57ns
Env x lin	5	0.0115	1.53ns
Env x quad	5	0.0178	2.37*
Env x dev	10	0.0090	1.20ns
Env x BSCB1(R)Cn	20	0.0136	1.81*
Env x lin	5	0.0151	2.01ns
Env x quad	5	0.0067	0.89ns
Env x dev	10	0.0164	2.19*
Env x BSSS(R)CnxBSCB1(R)Cn	10	0.0316	4.21**
Env x lin	5	0.0344	4.59**
Env x dev	5	0.0288	3.84**
Env x res	20	0.0217	2.89**
Pooled error	336	0.0075	

*,**Significant at the 0.05 and 0.01 level, respectively.

Table 26. Analysis of variance for the 15 entries combined over five environments with main effects partitioned to show the effects of cycles of selection on 300-kernel weight (g)

Source	d.f.	Mean squares	F-ratio
Environment (env)	5	3244.43	19.36**
Replications/env	24	167.60	6.41**
Entries (ent)	14	680.29	26.02**
BSSS(R)Cn	4	165.99	6.35**
Linear (lin)	1	220.78	8.45**
Quadratic (quad)	1	57.16	2.19ns
Deviations (dev)	2	193.02	7.38**
BSCB1(R)Cn	4	156.72	6.00**
Lin	1	359.07	13.74**
Quad	1	175.91	6.73*
Dev	2	44.45	1.70ns
BSSS(R)CnxBSCB1(R)Cn	2	135.66	5.19**
Lin	1	122.81	4.70*
Dev	1	148.51	5.68*
Residual (res)	4	2016.22	77.13**
Env x ent	70	35.14	1.34ns
Env x BSSS(R)Cn	20	18.10	0.69ns
Env x lin	5	13.68	0.52ns
Env x quad	5	30.90	1.18ns
Env x dev	10	13.91	0.53ns
Env x BSCB1(R)Cn	20	31.26	1.20ns
Env x lin	5	30.89	1.18ns
Env x quad	5	10.17	0.39ns
Env x dev	10	41.98	1.61ns
Env x BSSS(R)CnxBSCB1(R)Cn	10	24.80	0.95ns
Env x lin	5	35.78	1.37ns
Env x dev	5	13.88	0.53ns
Env x res	20	61.25	2.34**
Pooled error	336	26.14	

*,**Significant at the 0.05 and 0.01 level, respectively.

of the variation among entries with values ranging from 97% for grain yield to 59% for cob diameter. The linear model explained at least 85% of the variation among the entries for the other traits.

The linear and linear and quadratic regression coefficients from the two regression models are given in Tables 27 and 28. In most instances the linear regression coefficients were significant and the quadratic regression coefficients were not significant. A significant quadratic coefficient indicates a nonlinear response from selection for that trait.

Seven cycles of reciprocal recurrent selection produced no significant change in grain yield in the populations themselves. The population cross increased 1.75 ± 0.37 q/ha (2.98%) per cycle in grain yield. There was no indication rate of improvement in the population cross was declining, as deviations from linear regression were not significant. This observed yield gain was less than the 2.73 q/ha (4.6%) per cycle increase reported by Eberhart et al. (1973) and greater than the 1.18 q/ha (1.7%) per cycle reported by Penny and Eberhart (1971) in earlier evaluations of the same reciprocal recurrent selection program. Fakorede (1977) reported a 2.06 q/ha per cycle gain in grain yield when averaged across nitrogen levels, plant densities, and environments. Eberhart et al. (1973) observed no change in yielding ability of the two populations themselves after five cycles, but Penny and Eberhart (1971) found a slight increase in the BSSS(R)

Table 27. Linear regression coefficients of all traits measured for the BSSS(R)Cn and BSCB1(R)Cn populations and the BSSS(R)CnxBSCB1(R)Cn population crosses

Trait	BSSS(R)Cn	BSCB1(R)Cn	BSSS(R)Cnx BSCB1(R)Cn
Yield	0.61±0.33	-0.57±0.33	1.75±0.37
Date silk	-0.32±0.08	0.38±0.08	-0.23±0.09
Plant height	0.62±0.31	-0.92±0.31	1.10±0.35
Ear height	-1.01±0.25	-0.97±0.25	-0.30±0.28
Top height	1.63±0.21	0.06±0.21	1.39±0.24
Ear length	0.14±0.04	-0.01±0.04	0.09±0.05
Ear diameter	-0.019±0.006	-0.017±0.006	0.015±0.007
Cob diameter	0.007±0.005	-0.002±0.005	0.004±0.005
Kernel depth	-0.017±0.006	-0.015±0.006	0.012±0.007
Ears per plant	0.015±0.004	0.009±0.004	0.017±0.005
300-kernel weight	0.47±0.16	0.52±0.16	0.39±0.18

population and no change in yield in the BSCB1(R) population after four cycles of reciprocal recurrent selection.

Yield is plotted against cycles of selection for both populations and the population cross in Figure 1. Yield heterosis between the two populations, expressed as a percent of the midparent, increased from 14.93% in the C_0xC_0 cross to 41.68% in the C_7xC_7 cross. The lack of improvement in the populations themselves is probably due in part to inbreeding

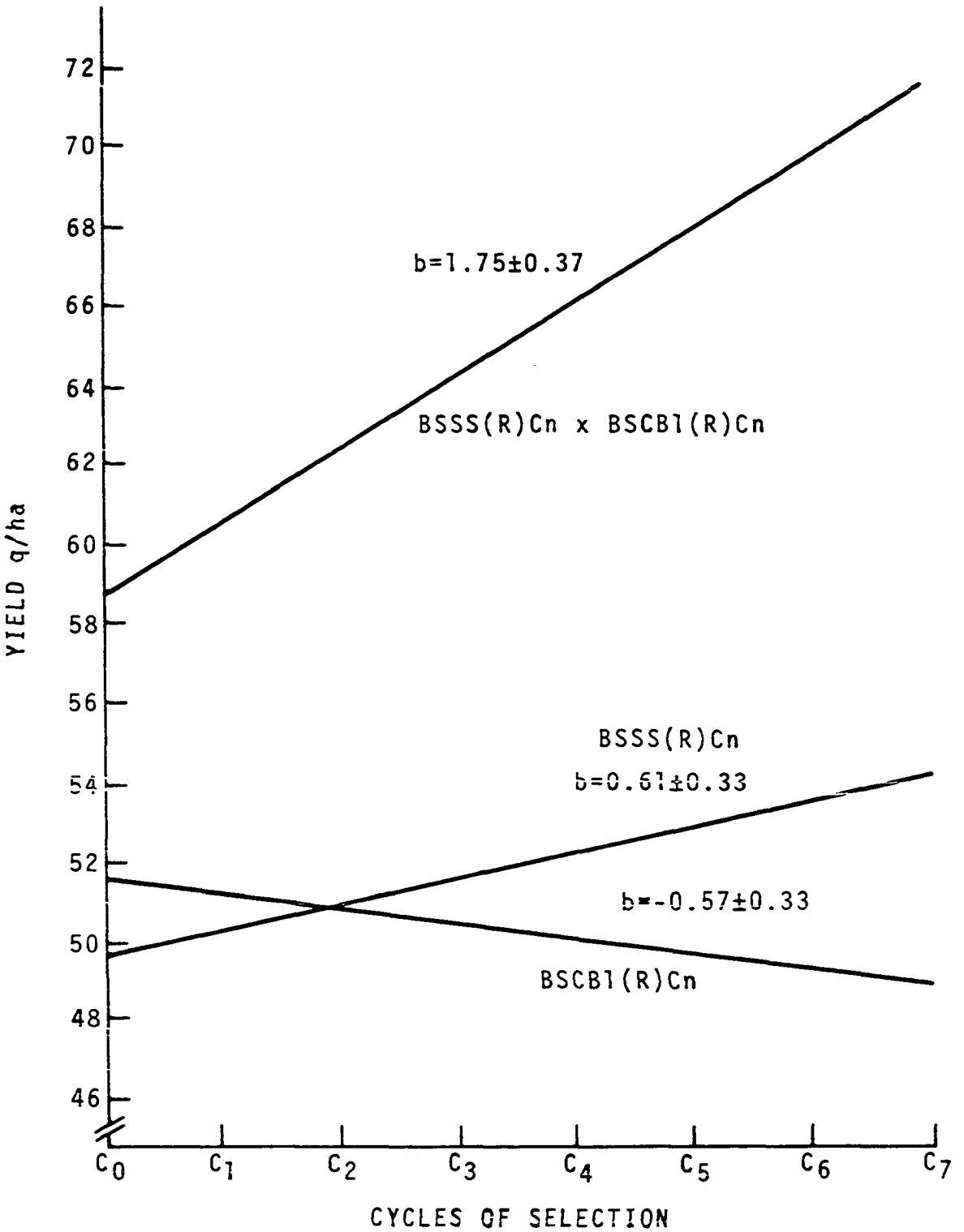
Table 28. Linear and quadratic regression coefficients of all traits measured for the BSSS(R)Cn and BSCB1(R)Cn populations

Trait	BSSS(R)Cn	BSCB1(R)Cn
Yield	1.54±1.23[a] -0.13±0.17[b]	1.02±1.23 -0.23±0.17
Date silk	-1.16±0.31 0.12±0.04	1.20±0.31 -0.12±0.04
Plant height	-4.16±1.16 0.69±0.16	-1.03±1.16 0.02±0.16
Ear height	-4.59±0.93 0.52±0.13	0.61±0.93 -0.23±0.13
Top height	0.46±0.80 0.17±0.11	-1.61±0.80 0.24±0.11
Ear length	0.15±0.16 0.00±0.02	0.62±0.16 -0.09±0.02
Ear diameter	-0.080±0.025 0.009±0.003	-0.008±0.025 -0.001±0.003
Cob diameter	0.004±0.018 0.000±0.002	0.001±0.018 -0.009±0.002
Kernel depth	-0.008±0.022 -0.001±0.003	-0.069±0.022 0.008±0.003
Ears per plant	0.046±0.016 -0.004±0.002	0.024±0.016 -0.002±0.002
300-kernel weight	-0.37±0.61 0.12±0.08	-1.01±0.61 0.22±0.08

[a]Linear regression coefficients.

[b]Quadratic regression coefficients.

Figure 1. Average yield response for the BSSS(R) and BSCB1(R) populations and the BSSS(R)xBSCB1(R) population cross for seven cycles of reciprocal recurrent selection


72
70
68
66
64
62
60
58
56
54
52
50
48
46
YIELD q/ha
b=1.75±0.37
BSSS(R)Cn x BSCB1(R)Cn
BSSS(R)Cn
b=0.61±0.33
b=-0.57±0.33
BSCB1(R)Cn
C0
C1
C2
C3
C4
C5
C6
C7
CYCLES OF SELECTION

depression. The C_7 selection populations have an estimated inbreeding coefficient (F) of 0.29. Hallauer and Sears (1973) reported a 0.44 q/ha decline in yield with each percent inbreeding in the BSSS population.

Entry means for all traits measured combined over environments are listed in Table 29. Yield improvement in the population cross must be attributed to small but significant improvements in some yield component traits. Ear diameter was increased 0.015±0.007 cm per cycle in the population cross. Other ear traits in the population cross showed positive linear regression coefficients but did not exceed twice their standard errors. Hallauer (1971) reported positive genetic correlations among the ear traits and yield in BSSS(R)x BSCB1(R) progenies. Therefore, positive changes in ear traits are to be expected as a correlated response to selection for grain yield. Fakorede (1977) also found significant changes in ear traits in BSSS(R)Cn x BSCB1(R)Cn crosses. But some interactions with nitrogen levels and plant densities complicated the interpretation.

Ear length in the BSSS(R) population was the only ear trait that showed significant improvement from selection in the populations themselves. Both kernel depth and ear diameter were significantly decreased in both populations. The other ear traits showed no significant change from selection. Some ear traits exhibited significant quadratic regression coefficients in one or both populations. The negative changes

Table 29. Entry means combined over environments for all traits

Entry	Yield, q/ha	Days to 50% silk[a]	Plant height, cm	Ear height, cm
$BSSSC_0$	50.0	25.8	200.1	101.0
$BSSS(R)C_1$	49.1	24.5	189.0	93.2
$BSSS(R)C_3$	51.5	22.3	187.0	89.4
$BSSS(R)C_5$	55.0	23.9	199.4	91.6
$BSSS(R)C_7$	52.4	23.0	198.7	91.6
$BSCB1C_0$	51.8	19.5	192.3	88.4
$BSCB1(R)C_1$	51.3	20.7	190.7	86.1
$BSCB1(R)C_3$	53.2	22.6	191.8	87.9
$BSCB1(R)C_5$	50.4	22.1	185.2	84.9
$BSCB1(R)C_7$	47.4	22.4	186.8	80.3
$BSSSC_0 \times BSCB1C_0$	58.5	22.5	203.6	99.5
BS13	55.6	25.2	185.3	94.8
$BSSS(M)C_6$	54.5	28.0	226.3	123.4
$BSSS(R)C_5 \times BSCB1(R)C_5$	67.4	21.7	208.0	99.9
$BSSS(R)C_7 \times BSCB1(R)C_7$	70.7	20.8	211.7	96.8
	54.6	23.0	197.1	93.9
S.E. mean	1.89	0.48	1.79	1.44

[a]Days from July 1.

Top height, cm	Ear length, cm	Ear diameter, cm	Cob diameter, cm	Kernel depth, cm	Ears per plant	Kernel weight, g
99.1	16.8	4.7	2.8	1.8	0.89	77.9
95.9	16.5	4.5	2.7	1.8	0.98	73.3
97.6	16.8	4.5	2.8	1.8	1.01	76.2
107.9	17.7	4.5	2.8	1.7	1.01	78.8
107.1	17.4	4.5	2.8	1.7	1.02	78.8
103.9	18.4	4.4	2.7	1.7	0.97	69.0
104.6	17.9	4.4	2.8	1.6	0.99	69.7
104.0	19.1	4.4	2.8	1.6	1.03	69.2
100.3	19.1	4.3	2.8	1.5	1.03	69.0
100.5	17.7	4.3	2.7	1.6	1.04	73.9
104.2	18.6	4.5	2.8	1.7	0.98	79.2
90.5	16.7	4.5	2.9	1.7	1.09	82.9
102.9	18.0	4.8	2.9	1.8	0.96	79.9
108.2	19.4	4.6	2.9	1.7	1.11	77.9
114.9	19.1	4.6	2.8	1.8	1.09	81.7
103.1	18.0	4.5	2.8	1.7	1.01	75.7
1.23	0.25	0.038	0.028	0.033	0.024	0.93

in some ear traits also may be due to inbreeding depression.

Ears per plant increased 0.015±0.004, 0.009±0.004, and 0.017±0.005 in the BSSS(R), BSCB1(R), and BSSS(R)Cn x BSCB1(R)Cn populations, respectively. Eberhart et al. (1973 and Fakorede (1977) found similar increases in ears per plant with the same genetic material. Hallauer (1974) studied the inheritance of prolificacy in maize and concluded it fit the description of a threshold character; that is, its phenotypic expression is discrete but the genetic and environmental variables controlling ear number are continuous. If prolificacy was controlled by mostly recessive loci, increasing the frequency of these recessive loci in the populations themselves would make for increased prolificacy in the populations and their cross as well.

Small but significant increases in 300-kernel weight were observed in both populations and the population cross. There was a significant quadratic effect in the BSCB1(R)Cn populations. Increased seed weight contributed to the yield increase in the population cross but the increase in seed weight was apparently offset by negative changes in the other yield component traits in the populations themselves.

Reciprocal recurrent selection reduced the number of days after July 1, to 50% silk emergence in the population cross (-0.23±0.09 days per cycle) and in the BSSS(R) populations (-0.32±0.08 days per cycle). Days to 50% silk emergence was significantly increased (0.38±0.08 days per cycle) in the

BSCB1(R) populations. Significant quadratic trends were found for both populations. The C_7 selection populations have almost identical silking dates. Because plants in each population were mated to plants in the opposite population to form the testcrosses, the changes in silking dates in the populations themselves may be an artifact of mating plants with similar silking dates. Eberhart et al. (1973) and Fakorede (1977) found no significant changes in silking date for the BSSS(R)Cn and BSCB1(R)Cn selection populations and BSSS(R)Cn x BSCB1(R)Cn crosses.

Plant height in the BSSS(R)Cn x BSCB1(R)Cn crosses increased 1.10±0.35 cm per cycle but ear height did not change. The additional plant height was added to internodes above the ear, as top height was increased 1.39 ±0.39 cm per cycle. Plant and ear height decreased -0.92±0.31 and -0.97±0.25 cm per cycle, respectively, in the BSCB1(R)Cn selection populations. Top height did not change significantly in the BSCB1(R)Cn selection populations. Plant height in the BSSS(R)Cn selection populations decreased then increased with the net result being the C_0 and C_7 selection populations were not different in plant height. Consequently, there was a significant quadratic effect for plant height in the BSSS(R)Cn populations (Table 28). Ear height declined 1.01±0.25 cm per cycle while top height increased 1.63±0.21 cm per cycle in the BSSS(R)Cn populations. Similar to plant height, ear height also showed a significant quadratic response

with cycles of selection (Table 28). These findings are in general agreement with those of Eberhart et al. (1973) and Fakorede (1977).

Changes in the BSSS population from mass selection (BSSS(M)C_6) and half-sib selection followed by S_1 selection (BS13) were assessed by comparing the BSSS(M)C_6 and BS13 entries with the BSSS(R)C_0 entry with the standard t-test. Significant, positive ($P < .05$) responses were detected for grain yield, cob diameter, ears per plant, and 300-kernel weight for the BS13 entry, while plant height, ear height, top height, ear diameter, and kernel depth decreased significantly. BS13 showed no change for date of 50% silk and ear length. The BSSS(M)C_6 entry was significantly greater than the BSSS(R)C_0 for date of 50% silk, plant height, ear height, ear length, cob diameter, and ears per plant. Six cycles of mass selection did not change yield, top height, ear diameter, kernel depth, and 300-kernel weight.

The alternative selection methods used to develop the BSSS(M)C_6 and BS13 entries provide an interesting comparison with reciprocal recurrent selection. The BS13 entry improved in yield over the original BSSS population despite an inbreeding coefficient greater than that in the BSSS(R)C_7 selection population. Half-sib and S_1 selection increased the frequency of alleles with partial to complete dominance controlling grain yield. It was not possible to separate the relative importance of half-sib selection versus S_1 selection

in this study. However, Eberhart et al. (1973) found a significant increase in grain yield in the BSSS population from seven cycles of half-sib selection.

Although ear traits increased with mass selection, grain yield did not increase after six cycles of selection. With mass selection the most phenotypically superior ears were selected. Phenotypic selection is not efficient when heritability is low, as in the case for grain yield in BSSS.

The results of my study and other evaluations of reciprocal recurrent selection method for yield improvement with BSSS and BSCB1 populations have shown that reciprocal recurrent selection was an effective method for improving the population cross for yield. It was not an effective method for improving the populations themselves. These results are not unlike those from other reciprocal recurrent selection programs. Moll and Stuber (1971) obtained 3.5% gain per cycle in grain yield in the Jarvis x Indian Chief cross following six cycles of reciprocal recurrent selection with these two populations. The Jarvis population increased slightly in yield, but no yield improvement was observed in the Indian Chief population. Similarly, most of the other evaluations of reciprocal recurrent selection have reported improvements in the population cross but little or no change in one or both source populations (Thomas and Grissom, 1961; Douglas et al., 1961).

The lack of improvement in the populations themselves found in this and other studies is disappointing but not

entirely unexpected. Comstock et al. (1949) emphasized that the objective of reciprocal recurrent selection is to improve the hybrid performance of the two source populations. Any improvement in the populations themselves is merely a correlated response with the hybrid improvement. Although the BSSS(R) and BSCB1(R) populations have not improved in yielding ability, they quite likely have been improved as sources of inbred lines. Some recessive loci may have been fixed due to inbreeding, while selection produced small increases in the frequency of the favorable allele at many other loci. The end result is that although mean frequency of the favorable allele in the populations may have increased, the mean performance has not changed.

Predicted Gains from Selection

The BSSS(R)C_0xBSCB1(R)C_0 testcrosses were grown in 1950 and the BSSS(R)C_7xBSCB1(R)C_7 testcrosses were evaluated in 1976. Approximately 100 testcrosses from each population were evaluated in each selection cycle, and 10 superior genotypes were recombined to form the new populations. The number of yield trials has varied from one in the C_0xC_0 testcrosses to four in the C_2xC_2, C_4xC_4, and C_5xC_5 testcrosses. Either two or three replications were used in each yield trial. As mentioned previously, the first four cycles of this reciprocal recurrent selection program were conducted according to the procedure outlined by Comstock et al. (1949). Major changes

were initiated at the start of the fifth cycle. Yield test trials were machine harvested rather than harvested by hand. Also, one generation of selfing preceded the forming of the testcrosses. Tables 30 and 31 summarize estimates of variance components obtained from the testcross yield trial data in each selection cycle.

The testcrosses were always evaluated in separate experiments, but both sets of testcrosses were grown at the same locations in a given selection cycle. Experimental error variances were of similar magnitude for both populations for corresponding selection cycles. Experimental error variances increased dramatically at the C_5 selection cycle corresponding with the change from hand to machine harvesting.

Because the testcrosses were evaluated in only one environment in the initial selection cycle, the genotypic variances (σ^2_G) are inflated by the genotype x environment (σ^2_{GxE}) in the C_0 selection cycle. The low genotypic variances in both populations for the C_1, C_2, C_3, and C_4 selection cycles are in part what prompted Penny and Eberhart (1971) to impose one generation of selfing on the pollen parents before forming the testcrosses. Quantitative genetic theory states genotypic variance among testcross progenies is increased by inbreeding. Rawlings and Thompson (1962) expressed variance among testcross progenies in terms of gene frequencies as $\sigma^2_G = \frac{1}{2}p(1-p)(1+F)[1+(1-2r)a]^2u^2$, where

Table 30. Summary of variance components and heritability estimates for yield for the BSSS(R) selection populations obtained from testcross yield trials

Selection population	Year	No. of trials	Reps/ trial	Variance component estimates σ^2	σ^2_{GxE}	σ^2_G	Herita-bility
BSSS(R)C_0	1950	1	3	27.9±3.0	-	13.3±3.4	58.8
BSSS(R)C_1	1953	2	3	33.1±2.3	0.1±1.7	11.1±2.5	66.7
BSSS(R)C_2	1956-57	4	2.7[a]	41.4±2.2	3.3±1.7	3.9±1.2	45.5
BSSS(R)C_3	1960	2	3	24.5±1.7	4.0±1.8	4.2±1.7	40.8
BSSS(R)C_4	1964	4	2	30.2±2.4	3.0±2.0	2.0±1.0	30.6
BSSS(R)C_5	1970	4	2	64.6±4.1	4.6±4.7	13.2±3.3	58.9
BSSS(R)C_6	1973	3	2	70.6±4.5	14.0±5.9	15.6±5.5	48.1
BSSS(R)C_7	1976	3	2	106.3±6.8	12.5±8.1	13.4±5.4	38.0
Mean C_1-C_4		2.7[a]	2.6[a]	32.3±2.2	2.6±1.8	5.3±1.6	45.9
Mean C_5-C_7		3.3[a]	2.0[a]	80.5±5.1	10.4±6.2	14.1±4.7	48.3
Mean C_0-C_7		2.3[a]	2.4[a]	49.8±3.4	5.9±3.7	9.6±3.0	48.2

[a]Values are harmonic means.

Table 31. Summary of variance component and heritability estimates for yield for the BSCB1(R) selection populations obtained from the testcross yield trials

Selection population	Year	No. of trials	Reps/ trial	Variance component estimates σ^2	σ^2_{GxE}	σ^2_G	Herita-bility
BSCB1(R)C_0	1950	1	3	14.9±1.6	-	20.8±3.7	80.7
BSCB1(R)C_1	1953	2	3	34.1±2.8	2.3±2.3	16.9±3.8	71.2
BSCB1(R)C_2	1956-57	4	2.7[a]	43.1±2.2	4.6±1.7	2.8±1.1	37.1
BSCB1(R)C_3	1960	2	3	26.0±1.9	7.5±2.4	6.8±2.4	45.7
BSCB1(R)C_4	1964	4	2	23.5±1.8	5.8±1.8	5.7±1.5	56.7
BSCB1(R)C_5	1970	4	2	87.6±5.8	12.1±6.8	11.0±3.8	44.0
BSCB1(R)C_6	1973	3	2	81.3±5.2	11.6±6.4	32.9±8.8	65.3
BSCB1(R)C_7	1976	3	2	85.4±4.5	12.9±6.8	20.8±5.8	52.9
Mean C_1-C_4		2.7[a]	2.6[a]	31.7±2.2	5.1±2.1	8.1±2.2	52.7
Mean C_5-C_7		3.3[a]	2.0[a]	84.8±5.2	12.2±6.7	21.6±6.1	54.1
Mean C_0-C_7		2.3[a]	2.4[a]	49.5±3.3	8.1±4.0	14.7±3.9	56.7

[a]Values are harmonic means.

p = frequency of the favorable allele in the material being tested,

F = inbreeding coefficient in the material being tested,

r = frequency of the favorable allele in the tester,

a = level of dominance, and

u = one-half the difference between the two homozygous genotypes.

The generation of selfing has been successful in increasing genotypic variance in both populations; in fact, the genotypic variances have increased more than (1+F). In general, genotypic variance components were larger in the BSCB1(R) population. From the variance component estimates there is no indication that genotypic variances have declined with selection in either population.

Genotype x environment interactions were of similar magnitude in both populations for corresponding cycles of selection. In some instances the interaction variances were equally as large as the genotypic variances. The genotype x environment interactions also increased when one generation of selfing was imposed. Horner et al. (1973) also observed greater genotype x environment interaction among testcrosses with more inbred material.

Heritability values calculated on a family mean basis showed no consistent change with cycles of selection in either population. Heritabilities were higher in the BSCB1(R) population reflecting larger genotypic variance in that population.

Because selection and evaluation procedures were most similar within the C_1 to C_4 and C_5 to C_7 selection cycles, it seemed logical to average variance components over these cycles of selection for each population. Variance components were also averaged over all selection cycles. The average variance components and heritability values also are presented in Tables 30 and 31.

The variance component estimates were used to predict gain per cycle from reciprocal recurrent selection. The appropriate estimates were substituted into the formula cited previously. From the formula it is seen that gain from reciprocal recurrent selection is the sum of gain contributed by each population to the population cross. Expected gains were calculated using variance estimates from each individual selection cycle, average of C_1 to C_4 selection cycles, average of C_5 to C_7 selection cycles, and average of C_0 to C_7 selection cycles. Predicted gains per cycle for the population cross along with contributions from each population are given in Table 32.

When variance components from individual selection cycles were substituted in the formula, expected gain ranged from 4.11 to 9.46 q/ha per cycle. Expected gain per cycle was 6.53 q/ha for the C_1 to C_4 averages, 10.65 q/ha for the C_5 to C_7 averages, and 8.20 q/ha for the C_0 to C_7 averages. Generally, the BSCB1(R) population contributed more than the BSSS(R) population to the predicted gain in the population cross.

Variance component estimates in the original BSSS popula-

Table 32. Predicted gain per cycle from reciprocal recurrent selection using different combinations of the variance component estimates

Variance component estimates	Contribution from BSSS(R)	Contribution from BSCB1(R)	Gain per cycle
C_1-C_2	4.76	3.47	8.23
C_2-C_3	2.33	1.78	4.11
C_3-C_4	2.29	3.08	4.37
C_4-C_5	1.37	3.14	4.51
C_5-C_6	4.88	3.85	8.73
C_6-C_7	4.82	4.64	9.46
Average of			
C_1-C_4	2.81	3.72	6.53
C_5-C_7	4.55	6.12	10.67
C_0-C_7	3.64	4.56	8.20

tion obtained from Design I and II experiments (Silva and Hallauer, 1975) were used to calculate expected gain per cycle from mass selection. Substitution of the appropriate variance component estimates into the formula cited previously gave a predicted gain of 1.29 q/ha per cycle.

The predicted gains from reciprocal recurrent and mass selection are greater than the observed gains reported in this study. Moll and Robinson (1966) reported good agreement between observed and predicted gains for grain yield in the

Jarvis x Indian Chief population cross following four cycles of reciprocal recurrent selection. Similarly, Darrah et al. (1972) found good agreement between observed and expected yield improvement from reciprocal recurrent selection in Kenya, East Africa. In other long-term selection studies in maize, Burton et al. (1971) found observed gains of 1.2 q/ha per cycle from half-sib selection and 3.6 q/ha per cycle from S_1 selection in the BSK population. Predicted gains were 5.7 q/ha and 8.2 q/ha per cycle from half-sib and S_1 selection, respectively. After seven cycles of half-sib selection in the BSSS population with Ial3 as tester Eberhart et al. (1973) observed 1.63 q/ha per cycle increase in yield compared with a predicted gain of 3.17 q/ha per cycle. With reciprocal full-sib selection in BS10 and BS11 populations, Obilana (1977) reported a 7.33% per cycle gain in yield in the population cross while predicted gain was 12.33% per cycle. Compton and Bahadur (1977) found 5.26% per cycle gain in grain yield for 10 cycles of ear-to-row selection. Predicted gain was 4.87% per cycle. In general it seems observed improvements are about equal to or less than predicted gains from selection.

The large disparity between predicted and observed yield gains from this reciprocal recurrent selection program might be because genotypic variances are inflated beyond their actual values relative to the other variance estimates. Comstock and Moll (1963) pointed out inadequate estimates of

genotype x environment interaction can inflate genotypic variance estimates.

Testcross yield trials have been conducted in a minimum of one and a maximum of four environments. Perhaps more extensive testing would have estimated the true genetic differences more accurately. The yield trials for a given cycle were all conducted in only one year at more than one location, and the locations within a year were considered random environments. Comstock and Moll (1963) and experience in Iowa have shown genotype x year and genotype x location interactions are generally similar, and both these first-order interactions were smaller than the second-order interaction. Therefore, each location-year combination can be treated as an environment. If the genotype x year interaction was larger than the location x year interaction, then genotypic variances would be inflated causing predicted gains to be overestimated.

All yield trial plots have been harvested by machine since the C_5 selection cycle. The criterion for selection is yield of grain harvested, not yield of grain produced. Machine harvesting in effect places selection pressure on grain yield plus root and stalk lodging and ear retention. Some attention, however, also was given to lodging resistance in early selection cycles. Simultaneous selection for yield and other agronomic traits would reduce rate of improvement for grain yield, especially if traits were negatively correlated with yield. Penny and Eberhart (1971) have reported negative

correlations between yield and stalk lodging in the BSSS(R)C_5x BSCB1(R)C_5 testcrosses.

Genotypic variances are defined in terms of gene frequencies and are expected to change with selection. Predicted gains would be greater than observed gains if the genetic variability had been depleted by selection. Furthermore, declining genotypic variance would result in a declining rate (curvilinear) of observed response to selection. Variance components shown in Tables 30 and 31 indicated genotypic variance was not depleted by selection. Hallauer (1971) reported no change in genotypic variance estimates in the BSSS(R) and BSCB1(R) populations after four cycles of reciprocal recurrent selection. Rate of yield improvement in the population cross was linear. Evidence suggests declining genotypic variance was not a probable cause for the discrepancy between observed and predicted gains in this study.

The formula for predicted gain from selection assumes no linkage and no epistasis. These assumptions may not be valid. Two generations of intermating were probably not sufficient to bring the selection populations to linkage equilibrium. Theoretically, the effect of linkage is to bias upwards (when in coupling phase) and downwards (when in repulsion phase) estimates of σ^2_G. If genotypic variance estimates were biased upwards due to linkage, predicted gains would have been overestimated.

If epistasis is operating, then the effect of an allele

is conditioned by the presence of alleles at other loci. It seems unlikely that epistatic type gene action could account for lack of agreement between observed and predicted responses. Silva and Hallauer (1975) attempted to estimate epistatic variance components in the BSSS population. They obtained large negative variance estimates when more than one epistatic term was included in the model.

The standardized selection differential, K, is calculated as $\frac{(\bar{\bar{X}}_S - \bar{X})}{\sigma_p}$, where $\bar{\bar{X}}_S$ is the mean of the selected genotypes, $\bar{X}$ is the mean of all genotypes and σ_p is the phenotypic standard deviation of the testcross means. It is convenient to express the selection differential in this manner because K can be obtained for any selection intensity by dividing the ordinate (Z) from the normal curve by the selection intensity expressed as a percentage. However, the calculation of K assumes the testcross means are normally distributed. If the testcross means are not normally distributed and skewed to the right, the standardized selection differential, K, would be larger than the true value. This would lead to overestimation of predicted gain.

Computer Simulation

Six sets of starting conditions were imposed on the initial populations by imposing three levels of dominance at each of two gene frequencies in the populations. Duplicate

runs for each starting condition were made by using different seeds to generate random numbers and reordering the genotypes in the initial populations. Ten cycles of reciprocal recurrent selection were simulated for each condition.

Genotypic means in the populations themselves and in the population cross were calculated for each selection cycle. The mean frequency of the favorable allele in the populations themselves was also calculated for each selection cycle by averaging the frequencies from the 40 loci. The populations themselves and population crosses from each selection cycle were treated as entries and the genotypic means and frequency means were analyzed using conventional analysis of variance procedures. This analysis was done to obtain a "rough error" to use in calculating standard errors for means and regression coefficients. This type of analysis is valid only if entry variances are homogeneous across selection cycles.

The analysis of variance table for genotypic means for each starting condition is given in Table 33. The entries mean square was highly significant ($P < .01$) for all starting conditions. The replication mean squares were significant at the 5% level for conditions 1 and 6 and significant at the 1% level for condition 3. The error mean squares were similar but generally were greater when the starting frequencies in the populations were different (conditions 4, 5, and 6) at a given level of dominance.

There were highly significant ($P < .01$) differences among

Table 33. Analysis of variance of genotypic means from the simulated selection populations and population crosses for each starting condition

		Mean squares					
		Starting condition					
Source	d.f.	1	2	3	4	5	6
Replications	1	54.09*	0.30	282.39**	0.01	32.42	146.11*
Entries	32	190.77**	184.84**	646.61**	1577.75**	1109.89**	928.45**
Error	32	8.15	6.71	10.21	26.46	9.70	21.16

*,**Significant at the 0.05 and 0.01 level, respectively.

Table 34. Analysis of variance for mean gene frequency from the simulated selection populations for each starting condition

		Mean squares					
		Starting condition					
Source	d.f.	1	2	3	4	5	6
Replications	1	0.0032*	0.0019	0.0073**	0.00002	0.0022*	0.0038
Entries	21	0.1844**	0.2683**	0.5647**	1.6318**	1.2453**	0.9304**
Error	21	0.0005	0.0006	0.0005	0.0007	0.0003	0.0012

*,**Significant at the 0.05 and 0.01 level, respectively.

entries for mean gene frequency for all starting conditions (Table 34). Significant replication mean squares existed for starting conditions 1 and 5 at the 5% level and at the 1% level for starting condition 3. Error mean squares were similar for conditions 1, 2, 3, and 4. The error mean square for condition 5 was about half as large and that for condition 6 was about twice as large as the other conditions.

Linear and quadratic regression models were fitted to the simulated data to assess rate of progress with cycles of selection. Total genetic gain in the populations themselves and the population cross was expressed as a percentage of the C_0 or C_0xC_0 selection populations. The linear and linear and quadratic regression coefficients and the total genetic gain for both populations and the population cross for each starting condition are presented in Table 35. The linear regression coefficients were significant for all conditions. The linear model accounted for 86.04, 93.70, 93.86, 97.58, 97.89, and 96.41% of the variation for conditions 1, 2, 3, 4, 5, and 6, respectively. Although the linear model accounted for most of the variation, all quadratic regression coefficients were significant except for populations A and B in condition 2 and population A in condition 4. All significant quadratic regression coefficients have negative signs, indicating rate of response to selection declined with advancing selection cycles.

Greatest rates of improvement (largest linear regression coefficient) in the populations themselves and the population

Table 35. Regression coefficients obtained from the linear and quadratic models and percent gain from 10 cycles of simulated reciprocal recurrent selection

Starting condition	Model	Population A Regression coefficient	A % gain	Population B Regression coefficient	B % gain	Population AB Regression coefficient	AB % gain
1	Linear	0.57±0.19	8.16	0.43±0.19	6.69	3.36±0.19	22.98
	Quadratic	3.71±0.72 -0.31±0.07		2.43±0.72 -0.20±0.07		6.98±0.72 -0.36±0.07	
2	Linear	1.99±0.17	20.80	1.96±0.17	19.14	3.72±0.17	34.03
	Quadratic	3.07±0.65 -0.11±0.06		3.06±0.65 -0.11±0.06		5.27±0.65 -0.16±0.06	
3	Linear	6.15±0.22	74.59	4.08±0.22	50.31	5.13±0.22	62.94
	Quadratic	11.02±0.80 -0.49±0.08		7.27±0.80 -0.32±0.08		9.25±0.80 -0.41±0.08	
4	Linear	1.43±0.35	19.67	2.29±0.35	21.15	5.13±0.35	51.23
	Quadratic	1.17±1.29 0.03±0.12		4.83±1.29 -0.25±0.12		8.61±1.29 -0.35±0.12	
5	Linear	2.91±0.21	43.09	2.63±0.21	25.59	4.85±0.21	53.97
	Quadratic	4.81±0.78 -0.19±0.07		5.01±0.78 -0.24±0.07		8.32±0.78 -0.35±0.07	
6	Linear	5.86±0.31	134.43	4.42±0.31	55.29	5.16±0.31	83.22
	Quadratic	8.05±1.15 -0.22±0.08		7.43±1.15 -0.31±0.08		7.75±1.15 -0.26±0.08	

cross were obtained for starting conditions with no dominance (conditions 3 and 6). With no dominance rate of improvement in the hybrid was about midway between the rate of improvement in the A and B populations. Populations A and B showed different ($P < .05$) improvement rates in condition 3 and in condition 6. Changing the initial gene frequency in population A from 0.50 to 0.25 had no appreciable effect on rates of improvement (condition 3 versus condition 6).

With partial or complete dominance (conditions 1, 2, 4, and 5) hybrid improvement significantly ($P < .05$) exceeded improvement rate in the populations themselves. The populations themselves did not differ in rate of improvement within a condition with partial or complete dominance. When the initial gene frequency in population A was reduced from 0.50 to 0.25, rates of improvement were greater in both the hybrid and the populations themselves for a given level of dominance (conditions 1 and 2 versus conditions 4 and 5).

Total gains followed the same trends as rates of improvement. Increasing the level of dominance generally reduced the total percent gain. A greater percentage gain was observed in both populations and the population cross when the initial gene frequency was reduced from 0.50 to 0.25. It should be noted the gains are expressed as a function of the mean of the initial populations, and the means are lowest with low gene frequencies and no dominance.

The linear and quadratic regression models were also

fitted to the simulated genotypic means from each replicate run. The linear and linear and quadratic regression coefficients are found in Appendix A, Tables 43 and 44. The same trends were evident as were described previously. In general, however, it seems that hybrid response was more predictable than the populations themselves.

The simulated data for each starting condition is further summarized in Tables 36 to 41. Each table presents genotypic means, mean gene frequencies, and number of alleles fixed in both populations as well as genotypic means and heterosis, expressed as a precent of the midpoint, for the population cross in each selection cycle.

With equal initial gene frequencies in the populations, 10 cycles of reciprocal recurrent selection changed mean gene frequencies in the populations most in the condition with no dominance (condition 3). A smaller change in mean gene frequency was noted as the level of dominance was increased. The mean gene frequency values were nearly identical in populations A and B for conditions 1 and 2, but values were 0.87 in population A and 0.75 in population B for condition 3. This large disparity between the two populations was not expected in the no dominance condition.

When the initial gene frequency was reduced from 0.50 to 0.25 in population A, 10 cycles of selection changed the mean gene frequency in population A from 0.26 to 0.44, 0.50, and 0.63 for levels of dominance 1.00, 0.75, and 0.00, respectively.

Table 36. Genotypic mean ($\bar{X}$), mean frequency of favorable allele (P), and number of alleles fixed in the populations themselves, genotypic mean of the population hybrid, and percent heterosis in each selection cycle for starting condition 1

Selection cycle	Population A				Population B				AB	Percent heterosis
			Alleles fixed				Alleles fixed			
	$\bar{X}$	P_A	aa	AA	$\bar{X}$	P_B	aa	AA	$\bar{X}$	
0	118.9	0.56	0.0	0.0	119.5	0.50	0.0	0.0	119.3	0.07
1	126.4	0.54	0.0	0.0	128.8	0.56	0.0	0.0	127.3	-0.31
2	132.0	0.60	0.0	0.5	128.6	0.60	0.5	1.0	134.5	4.18
3	131.8	0.62	0.0	1.0	129.9	0.62	1.0	2.0	138.6	7.76
4	130.3	0.65	0.5	5.0	127.1	0.64	1.5	4.5	143.1	14.14
5	130.4	0.67	0.5	7.5	129.1	0.67	1.5	7.0	146.5	16.74
6	133.3	0.69	1.0	8.0	130.1	0.68	2.5	10.0	148.5	16.83
7	132.6	0.69	1.5	9.0	129.9	0.70	2.5	13.0	151.1	19.83
8	129.0	0.68	2.0	10.0	130.0	0.70	2.5	15.0	152.1	22.65
9	131.1	0.70	2.0	12.0	128.9	0.71	3.0	15.5	154.5	24.51
10	128.6	0.70	2.5	14.5	127.5	0.71	3.5	17.5	154.9	26.83
S.E. $\bar{X}$	2.02	0.016			2.02	0.016			2.02	

Table 37. Genotypic mean ($\bar{X}$), mean frequency of favorable allele (P), and number of alleles fixed in the populations themselves, genotypic mean of the population hybrid, and percent heterosis in each selection cycle for starting condition 2

Selection cycle	Population A				Population B				AB	
			Alleles fixed				Alleles fixed			
	$\bar{X}$	P_A	aa	AA	$\bar{X}$	P_B	aa	AA	$\bar{X}$	Percent heterosis
0	109.6	0.50	0.0	0.0	109.2	0.49	0.0	0.0	109.3	-0.13
1	115.9	0.54	0.0	0.0	114.9	0.53	0.0	0.0	115.6	0.21
2	121.8	0.59	0.0	0.5	116.2	0.56	0.5	0.0	120.8	1.50
3	122.0	0.60	0.0	1.0	118.0	0.58	0.5	0.5	124.o	3.46
4	121.9	0.62	0.5	2.5	121.6	0.62	1.0	2.5	128.0	5.17
5	122.6	0.63	1.0	3.0	122.1	0.64	1.0	5.0	131.0	7.06
6	125.5	0.67	1.0	3.5	125.4	0.67	1.0	8.0	135.8	8.32
7	128.3	0.70	1.5	6.0	125.5	0.69	1.0	10.0	139.8	10.12
8	130.6	0.73	1.5	10.0	127.9	0.71	1.5	11.0	143.1	10.69
9	131.4	0.74	2.5	12.5	129.2	0.72	1.5	15.5	145.0	11.26
10	132.4	0.75	2.5	15.5	130.1	0.74	2.0	17.5	146.5	11.54
S.E. $\bar{X}$	1.83	0.017			1.83	0.017			1.83	

Table 38. Genotypic mean ($\bar{X}$), mean frequency of favorable allele (P), and number of favorable alleles fixed in the populations themselves, genotypic mean of the population hybrid, and percent heterosis in each selection cycle for for starting condition 3

Selection cycle	Population A				Population B				AB	Percent heterosis
			Alleles fixed				Alleles fixed			
	$\bar{X}$	P_A	aa	AA	$\bar{X}$	P_B	aa	AA	$\bar{X}$	
0	79.9	0.50	0.0	0.0	79.9	0.50	0.0	0.0	79.6	-0.37
1	89.8	0.56	0.0	0.0	86.6	0.54	0.0	0.0	88.3	0.08
2	100.8	0.63	1.0	0.5	91.3	0.57	0.0	0.0	95.8	-0.20
3	106.6	0.67	1.0	1.0	97.1	0.61	0.0	1.0	101.7	-0.14
4	111.3	0.70	1.0	5.0	103.3	0.65	0.5	2.5	107.7	0.40
5	122.4	0.76	1.5	10.0	109.7	0.69	1.0	5.0	116.2	0.13
6	130.1	0.81	1.5	14.5	111.6	0.70	1.5	9.5	120.5	-0.25
7	134.3	0.84	1.5	20.0	114.4	0.71	2.5	11.5	124.5	0.11
8	137.2	0.86	1.5	23.5	116.4	0.73	2.0	13.5	127.0	0.11
9	138.5	0.87	1.5	26.5	119.0	0.74	2.0	15.5	128.9	0.09
10	139.5	0.87	1.5	27.5	120.1	0.75	2.5	18.5	129.7	-0.09
S.E. $\bar{X}$	2.26	0.016			2.26	0.016			2.26	

Table 39. Genotypic mean ($\bar{X}$), mean frequency of favorable allele (P), and number of alleles fixed in the populations themselves, genotypic mean of the population hybrid, and percent heterosis in each selection cycle for starting condition 4

Selection cycle	Population A				Population B				AB	Percent heterosis
			Alleles fixed				Alleles fixed			
	$\bar{X}$	P_A	aa	AA	$\bar{X}$	P_B	aa	AA	$\bar{X}$	
0	73.7	0.27	0.0	0.0	119.6	0.50	0.0	0.0	101.5	5.03
1	77.6	0.29	1.0	0.0	126.1	0.55	0.0	0.0	111.1	9.09
2	76.5	0.30	4.0	0.5	132.3	0.61	0.5	1.0	118.2	13.29
3	75.4	0.32	4.0	1.0	135.4	0.65	0.5	2.5	125.5	19.06
4	79.8	0.35	7.0	1.0	137.2	0.69	0.5	6.0	131.6	21.33
5	82.6	0.37	8.0	1.5	138.1	0.72	0.5	9.0	136.6	23.72
6	82.2	0.38	8.0	2.0	139.5	0.74	0.5	11.0	140.4	26.61
7	82.8	0.39	9.5	3.0	142.2	0.78	0.5	12.5	144.7	28.71
8	85.7	0.41	10.0	4.0	143.6	0.81	0.5	19.5	149.5	30.43
9	87.3	0.43	10.5	4.0	145.1	0.83	0.5	21.0	152.0	30.92
10	88.2	0.44	10.5	5.5	144.9	0.84	1.0	24.0	153.5	31.66
S.E. $\bar{X}$	3.63	0.019			3.63	0.019			3.63	

Table 40. Genotypic mean ($\bar{X}$), mean frequency of favorable allele (P), and number of alleles fixed in the populations themselves, genotypic mean of the population hybrid, and percent heterosis in each selection cycle for starting condition 5

Selection cycle	Population A				Population B				Population AB	Percent heterosis
			Alleles fixed				Alleles fixed			
	$\bar{X}$	P_A	aa	AA	$\bar{X}$	P_B	aa	AA	$\bar{X}$	
0	65.9	0.27	0.0	0.0	109.8	0.50	0.0	0.0	91.9	4.55
1	70.9	0.30	0.0	0.0	119.2	0.57	0.0	0.0	102.1	7.45
2	76.6	0.33	0.0	0.0	122.0	0.61	1.0	1.0	108.5	9.24
3	76.7	0.35	2.0	0.0	126.1	0.65	1.0	3.0	114.8	13.28
4	82.3	0.39	3.5	1.5	128.2	0.68	1.0	5.5	120.5	14.42
5	84.4	0.41	5.5	1.5	130.0	0.70	1.0	8.5	125.8	17.32
6	87.2	0.44	6.5	3.5	132.3	0.73	1.0	13.0	130.2	18.62
7	91.4	0.47	7.0	3.5	134.6	0.75	1.0	14.0	133.4	18.00
8	94.8	0.50	7.0	5.5	138.2	0.79	1.0	16.5	137.2	18.19
9	93.3	0.50	7.5	7.5	138.8	0.81	1.5	21.0	139.9	20.56
10	94.3	0.52	8.0	11.5	137.9	0.81	1.5	22.0	141.5	21.89
S.E. $\bar{X}$	2.20	0.012			2.20	0.012			2.20	

Table 41. Genotypic mean ($\bar{X}$), mean frequency of favorable allele (P), and number of alleles fixed in the populations themselves, genotypic mean of the population hybrid and percent heterosis in each selection cycle for starting condition 6

Selection cycle	Population A				Population B				Population AB	Percent heterosis
			Alleles fixed				Alleles fixed			
	$\bar{X}$	P_A	aa	AA	$\bar{X}$	P_B	aa	AA	$\bar{X}$	
0	42.7	0.27	0.0	0.0	80.3	0.50	0.0	0.0	61.4	-0.18
1	48.3	0.30	1.5	0.0	85.8	0.54	0.0	0.0	67.1	0.18
2	55.8	0.35	3.0	0.0	93.5	0.58	1.0	0.5	74.5	-0.23
3	62.7	0.39	4.0	0.5	99.4	0.62	1.0	1.0	81.4	0.42
4	70.9	0.44	4.0	2.5	107.3	0.67	1.0	2.0	88.8	-0.24
5	76.8	0.48	5.0	5.5	110.4	0.69	1.5	4.0	93.7	0.05
6	82.8	0.52	5.5	5.5	111.9	0.70	2.0	6.5	97.5	0.13
7	87.7	0.55	6.0	7.0	116.8	0.73	2.0	9.0	102.2	-0.11
8	89.8	0.56	6.5	10.0	118.8	0.74	2.5	13.5	104.7	0.34
9	96.6	0.60	8.0	12.5	122.9	0.77	2.5	16.5	109.9	0.15
10	100.1	0.63	8.0	13.5	124.7	0.78	3.5	19.5	112.5	0.12
S.E. $\bar{X}$	3.25	0.024			3.25	0.024			3.25	

Similarly, mean gene frequency in population B was changed from 0.50 to 0.84, 0.81, and 0.78 as level of dominance declined from 1.00 to 0.00.

In most conditions about half or more of the 40 loci were fixed in the dominant or recessive condition in both populations after 10 cycles. Some loci were fixed in the recessive condition in all conditions despite selection pressure for the favorable allele. The most alleles were lost when the initial gene frequency in population A was reduced to 0.25. In condition 4 more alleles were lost than were fixed in the dominant condition (10.5 versus 5.5). More alleles were fixed in the dominant condition in population B when the initial gene frequencies differed with partial and complete dominance. However, about equal numbers of loci were fixed with no dominance (condition 3 versus condition 6). As expected the rate of fixation seemed to increase with cycles of selection.

Heterosis between the two populations was expressed with partial and complete dominance (conditions 1, 2, 4, and 5), and the heterosis increased with cycles of selection in all conditions. The percent heterosis was greater when the populations had different initial gene frequencies within a level of dominance (condition 1 versus 4 and condition 2 versus 5).

Although rate of progress is essential for long-term genetic gains, a high mean is of uppermost importance. The highest hybrid means occurred with complete dominance. The hybrid mean in the 10th selection cycle for condition 1 was

154.9 and 153.5 for condition 4. The maximum value of 160 was nearly attained with 10 cycles of reciprocal recurrent selection in the complete dominance case for both initial gene frequencies (conditions 1 and 4). Hybrid means were lowest with no dominance (conditions 3 and 6), and partial dominance, 0.75 (conditions 2 and 5), produced hybrid means intermediate between the two extremes.

Mean gene frequencies were increased in all instances. The populations themselves were improved most with no dominance (conditions 3 and 6). This is because each favorable allele added contributed an equal increment to the genotypic value. With complete dominance the maximum genotypic value could theoretically be attained if all loci were heterozygous; that is, a gene frequency of 0.50. In this situation, adding favorable alleles would not produce a change in the mean.

Falconer (1960) expressed heterosis between two populations on a single locus basis as $(p-r)^2a$, where

a = level of dominance,

p = frequency of favorable allele in population A, and

r = frequency of favorable allele in population B.

Therefore, for heterosis to exist there must be some level of dominance and different gene frequencies in the two populations. This expression explains why no heterosis was observed with no dominance (conditions 3 and 6) and the greater heterosis with different initial gene frequencies in the populations (conditions 1 and 2 versus 4 and 5). Heterosis between the popula-

tions increased with selection as did mean gene frequencies in the populations. This suggests that although the average gene frequencies in the populations were nearly equal in some cases, frequencies at individual loci were different in the two populations. That is, with partial and complete dominance the two populations were improved complementary to each other so as to maximize the hybrid between them.

The equation for predicted gain per cycle from reciprocal recurrent selection (Empig, Gardner, and Compton, 1972) can be used to explain the complementary improvement in the populations.

$$\Delta G = \frac{\frac{1}{2}K}{\sigma_p} \left(pq[1+(1-2r)a]^2u^2 + rs[1+(1-2p)a]^2u^2\right) \quad ,$$

where

ΔG = gain from one cycle of reciprocal recurrent selection,

K = standardized selection differential,

σ_p = phenotypic standard deviation of half-sib family means,

p = frequency of the favorable allele in population A,

r = frequency of the favorable allele in population B,

a = level of dominance, and

u = one-half the difference between the two homozygous genotypes.

The complementary improvement occurs because the selection pressure on alleles in population A depends on the magnitude of $pq[1+(1-2r)a]^2u^2$, and the pressure exerted on alleles in the B population depends on $rs[1+(1-2p)a]^2u^2$. With no

dominance the quantities in brackets are 1.0 so that selection pressure on alleles is independent of the frequency of alleles in the opposite population. When dominance exists, selection favors the dominant allele with the highest frequency. Once small differences in allele frequencies exist in the populations the differences become greater with selection; the result is increased heterosis in the population cross. Loci with the lower dominant allele frequency may be lost due to chance fluctuations, and, as a result, the full genetic potential may not be realized.

Genotypic and phenotypic variances among testcrosses were obtained for each population in all selection cycles. These variance estimates averaged over the duplicate runs are given in Appendix A, Tables 45 to 50. As cited earlier, the genotypic variance among testcrosses is

$$\sigma_G^2 = \tfrac{1}{2}pq(1+F)[1+(1-2r)a]^2u^2 .$$

Most differences in genotypic variances can be accounted for by changing gene frequencies and levels of dominance. The genotypic variance estimates are all inflated beyond their theoretical values. For example, with initial gene frequencies at 0.50 in both populations, the genotypic variance among testcrosses is expected to be 30.0 with any level of dominance. The genotypic variance could be inflated with partial or complete dominance because the gene frequencies at individual loci are not 0.50, and 1-2r is not zero. These deviations from the average value when squared and summed over

the 40 loci account for some of the upward bias when partial or complete dominance is present. Sampling error cannot account for the upward bias, as an equal number of values above and below the theoretical values would be expected from sampling. The same S_1 individual was mated to females in the opposite population to form the testcrosses. This assumes the gene frequency in the S_1 individual is representative of the gene frequency of all individuals within the S_1 line. Clearly, one individual could deviate considerably from the average gene frequency within an S_1 line. It seems likely these deviations from the average value could cause increased variability among the testcrosses.

The normal deviates added to each half-sib family mean were generated to have a mean of zero and variance 100. The difference, however, between the phenotypic and genotypic variance components was almost always greater than 100.

Predicted gains were calculated for the simulated selection for each cycle by substituting the variance components into the formula cited earlier. The predicted and actual advances in each cycle for the population cross also are presented in Tables 45 to 50 in Appendix A. The predicted gains were less than the actual gains for all starting conditions. In most instances the observed gains were less than one-half the predicted gain from cycle to cycle. The agreement between predicted and observed gains did not improve with advancing cycles of selection.

Cress (1965) also reported actual gains less than predicted gains in the population hybrid with simulated reciprocal recurrent selection. He did not measure actual variance among the testcrosses, but calculated variances using the initial gene frequencies. Actual gains per cycle were about one-half the expected gains in some instances. If the theoretical variance component values were used to calculate expected gains in this study, the results would have been more similar to Cress' results.

Correlations between Simulated and Field Results

The starting conditions were chosen to represent breeding situations that might be encountered in practice. Equal initial gene frequencies (conditions 1, 2, and 3) represent the condition where both populations were similar, or where the populations were subpopulations of a large population. Unequal initial gene frequencies corresponded to the cases where the populations were diverse, or where one population was improved with selection and the other was not improved. The three levels of dominance (0.00, 0.75, and 1.00) were chosen to represent situations that might be encountered with quantitative traits in maize.

The field and simulation results were correlated to determine which set of starting parameters best described the field observations. The BSSS(R) selection populations were considered the A population, and the BSCB1(R) selection populations

were considered as the B population for the correlation studies. The correlation coefficients between the field and simulated results for each starting condition are listed in Table 42. The highest correlation occurred for equal initial gene frequencies and complete dominance (condition 1). The correlation coefficients declined in succeeding conditions.

These correlations and the means of the BSSS(R) and BSCB1(R) selection populations indicate the two source populations have similar gene frequencies. Furthermore, the correlation values are additional evidence that loci with partial to complete dominance are most important in conditioning yield in maize.

The simulated populations themselves and population hybrids showed a curvilinear response with advancing cycles of selection because genetic variance was depleted in the populations. Response to selection was linear in the BSSS(R), BSCB1(R), and BSSS(R)xBSCB1(R) selection populations. No change in genetic variance was observed in the source populations. Additional cycles of selection would be expected to produce a quadratic response in the BSSS(R)Cn x BSCB1(R)Cn hybrid if the changes in gene frequencies were great enough to change genetic variances.

Neither the BSSS(R) nor the BSCB1(R) selection populations changed significantly in yield with selection, and only small improvements in the simulated populations themselves were noted with complete dominance. Heterosis, however,

Table 42. Correlations between actual and simulated responses from reciprocal recurrent selection

Starting condition[a]	Correlation coefficient
1	0.76**
2	0.60*
3	0.34
4	0.37
5	0.35
6	0.21

[a]Defined in Table 10.

*,**Significant at the 0.05 and 0.01 level, respectively.

between the populations increased with cycles of selection in the field and simulation studies. This is evidence that one source population has been improved complementary to the other to maximize the hybrid performance.

Reciprocal recurrent selection was designed to capitalize on specific gene combinations such as overdominance and certain types of epistasis. The field results show little evidence for any type of nonadditive gene action other than complete dominance for grain yield.

Computer simulation can be used as a tool to bridge the gap between existing theory and practice. By programming existing theory and assumptions into the model, simulation results can be used to point out situations where existing

theory is inadequate in explaining actual results. Much of the existing theory relies on cumbersome equations and infinite population sizes. Computer simulation eliminates the equations and imposes finite limits on population sizes. Population parameters can be easily changed in simulated populations, and makes it possible to simulate results by merely changing the starting parameters. In this way simulated selection experiments can be performed that would take decades in actual practice.

Computer simulation studies, however, do have limitations. Computer time and storage restrictions make it unfeasible to deal with population sizes and numbers of loci that are expected in actual practice. Certainly, more than 40 loci are involved in conditioning most quantitative traits, and selections usually are made from more than 110 genotypes in the source populations. The simulation of a complex biological system requires some simplifying assumptions. For example, in this study linkage and epistasis were ignored. In practice these factors must be contended with. These simplifications make computer simulation subject to the same restrictions as theoretical calculations. Although it is easy to change the initial population parameters to simulate different genetic situations, any generalizations from the specific sets of conditions is risky because of the restrictions of the model.

An attempt was made to simulate reciprocal recurrent

selection as it is conducted under field conditions. Despite the effort and seemingly reasonable results from the simulation studies, not all aspects of the field procedures could be simulated, and some of the assumptions made were not realistic. Under field conditions S_1 lines were evaluated for stalk rot resistance and first-brood European corn borer feeding. This agroromic selection has obvious merit, but it was not possible to simulate this type of selection. The simulated results would not be affected if stalk rot and European corn borer resistance were inherited independently of grain yield. Suwantaradon et al. (1975) reported small but positive genotypic correlations between these two traits and grain yield in a subpopulation of BSSS.

Genotypic value was taken to be the sum total of the 40 loci in the simulation studies. Grain yield (genotypic value in the field studies) is the sum of genetic, environmental, and interactions of these factors from planting until harvest. The genotypic value is certainly an oversimplification of grain yield.

The simulated results are informative and seem to be a reasonable approximation to a complex biological system. However, they should be interpreted with caution. Computer simulation can in no way be considered a substitute for field experiments.

GENERAL DISCUSSION

Reciprocal recurrent selection has improved the BSSS(R)Cn x BSCB1(R)Cn crosses 1.75 q/ha per cycle. The populations themselves have not changed significantly with selection. The populations themselves and the population crosses also were improved significantly with simulated reciprocal recurrent selection. Least improvement in the populations themselves was obtained with complete dominance. The field and simulated results both have shown that reciprocal recurrent selection is not an efficient method to improve the source populations themselves. Both simulated populations were improved considerably with no dominance. If a quantitative trait were controlled by only additive gene action, a selection system based on the performance of the genotype itself, such as S_1 testing, would be more efficient than progeny testing.

The lack of improvement in the populations themselves is disappointing but not entirely unexpected. Comstock et al. (1949) clearly stated reciprocal recurrent selection was designed to improve hybrid performance. Selection of superior genotypes to be recombined to form the new populations is based on hybrid performance. There is no direct selection pressure to improve the populations themselves. Any improvement in the populations themselves would be a correlated response to hybrid improvement. The magnitude and sign of the

correlated response depend on the covariances of the additive genetic effects in the populations and the additive genetic effects in the hybrid (Cress, 1967; Moll and Stuber, 1971). These covariances were nonnegative with partial to complete dominance; therefore, the populations themselves would be expected to improve with reciprocal recurrent selection for partial to complete dominance. With overdominance the sign of the covariances depends on the gene frequencies in the populations compared to the equilibrium gene frequency, (1+a)/2a, where a is the level of dominance. If the frequency of the dominant allele was on the same side of the equilibrium frequency, the covariances in both populations would be positive and both populations should improve with selection. On the other hand, if allele frequencies in populations A and B were on opposite sides of the equilibrium, the covariances are negative and the mean of both populations should decline. The lack of improvement in the BSSS(R) and BSCB1(R) populations was probably due to inbreeding depression and perhaps overdominance at some loci.

Mean gene frequencies changed appreciably in the simulated populations but only small changes in mean value were noted in some instances. Selection affects a change in the mean value by changing gene frequencies. It can be shown, however, that in some special situations small changes in gene frequencies produce no change in the mean. To illustrate these situations, the notation shown below will be used

(Eberhart and Gardner, 1966).

Genotype	Genotypic frequency	Genotypic value
AA	p^2	α
Aa	$2p(1-p)$	δ
aa	$(1-p)^2$	$-\alpha$

Let p_{oi} and p_{1i} designate the frequency of the favorable allele at the i^{th} locus before and after selection, respectively. Summing over loci, the mean before selection is

$$C_0 = \sum_{i=1}^{n} (2p_{oi}-1)\alpha_i + 2\Sigma p_{oi}(1-p_{oi})\delta_i \quad .$$

After selection, the mean is

$$C_1 = \sum_{i=1}^{n} (2p_{1i}-1)\alpha_i + 2\Sigma p_{1i}(1-p_{1i})\delta_i \quad .$$

Substituting $p_{oi} + \Delta p_i = p_{1i}$, we have

$$C_1 = \sum_{i=1}^{n} (2p_{oi}-1)\alpha_i + 2\sum_{i=1}^{n} \Delta p_i\alpha_i + 2\sum_{i=1}^{n} \Sigma\Delta p_{oi}(1-p_{oi})\delta_i + 2\sum_{i=1}^{n} \Delta p_i(1-2p_{oi})\delta_i - 2\sum_{i=1}^{n} p_i^2\delta_i \quad .$$

If $C_0 = u$ then

$$C_1 = u + 2\sum_{i=1}^{n} \Delta p_i\alpha_i + 2\Sigma\Delta p_i(1-2p_{oi})\delta_i - 2\sum_{i=1}^{n} \Delta p_i^2\delta_i \quad .$$

If there is no change from selection, then

$$C_1 - C_0 = 0 \qquad \text{and}$$

$$2\sum_{i=1}^{n} \Delta p_i\alpha_i + 2\sum_{i=1}^{n} \Delta p_i(1-2p_{oi})\delta_i - 2\sum_{i=1}^{n} \Delta p_i^2\delta_i = 0 \quad .$$

Solving for Δp_i, we have

$$\Delta p_i = \alpha_i/\delta_i + (1-2p_{oi}) \quad .$$

There are some special situations that are of interest. First, with no dominance there is no solution. That is, a change in gene frequency always produces a change in the mean. For p_{oi} at 0.50 there would be no change in mean value if $\Delta p_i = \alpha_i/\delta_i$. With $p_{oi} = 0.50$ and complete dominance Δp_i must equal α for no change in the mean to occur. This logic serves to illustrate that changes in gene frequency may occur without affecting the mean of the population appreciably. These special situations cited are of little value in practical breeding situations.

Mean gene frequencies and heterosis between the simulated populations increased with cycles of selection despite only small improvements in the populations themselves. Increased heterosis and no change in performance in the populations themselves also were noted in the field results. The mean frequency of the favorable alleles has probably increased in the BSSS(R) and BSCB1(R) populations. The implication is that the probability of isolating inbred lines and superior single-cross genotypes from these two populations has increased even though the yield has not changed. Russell and Eberhart (1975) reported BSSS(R)C_5S_2xBSCB1(R)C_5S_2 crosses yielded as well or better than elite single-cross checks. Moll, Bari, and Stuber (1977) showed six cycles of reciprocal recurrent selection improved the chances of obtaining superior single-crosses. They found that the mean of the single-crosses from the improved populations was greater than the mean of the single-

crosses derived from the original populations, but the range in yield was similar for the two groups of single-crosses. Hoegemeyer and Hallauer (1976) also found single-crosses from improved populations yielded more than single-crosses from the corresponding unimproved populations.

Lack of improvement in the BSSS(R) and BSCB1(R) populations is due in part to inbreeding depression resulting from finite population sizes. Inbreeding leads to chance fixation of undesirable alleles, loss of favorable alleles, and loss of genetic variability. The end result is that the full genetic potential of the populations may never be realized. The computer simulation studies point out the effect of small population sizes and random fixation of alleles. Some favorable alleles were lost in all conditions despite selection pressure for the favorable allele, and alleles are not easily maintained at low frequencies.

The effects of inbreeding can be minimized by maintaining larger population sizes. Ten lines have been recombined to form the new selection populations in each cycle of selection. Inbreeding could be minimized by recombining more than 10 lines, but more testcrosses would need to be evaluated to maintain the same selection intensity. Resources needed to maintain population sizes large enough to minimize inbreeding may exceed practical limitations. Reciprocal full-sib selection has an advantage over reciprocal recurrent selection in that the same selection intensity can be maintained with only

one-half the number of testcrosses needed for evaluation.

Cress (1967) and Russell and Eberhart (1975) proposed reciprocal recurrent selection be modified by using inbred lines derived from the source populations as testers rather than the populations themselves. The idea has merit because this and other studies have shown nonadditive gene action other than complete dominance is not of major importance in conditioning grain yield. Furthermore, Horner et al. (1973), Russell, Eberhart, and Vega (1973), and Walejko (1976) all have shown hybrid performance of populations was improved with an inbred tester, and the improvement was not specific to the inbred tester used.

The greatest selection pressure for an allele in a population is exerted when the tester is fixed for the recessive allele. An inbred line would probably have alleles fixed in the recessive condition that are maintained at low frequencies in the source population from which it was derived. Therefore, greater selection pressure would be exerted for the favorable allele in the opposite population with an inbred tester if the inbred line was properly chosen.

Reciprocal recurrent selection promotes complementary improvement in the two source populations. Alleles present at high frequencies in one population probably will occur at lower frequencies in the other population. It seems likely, therefore, that inbreds derived from one source population would have different alleles fixed in the recessive condition

than inbreds derived from the opposite population. If this is true, the use of an inbred from each population as tester would accelerate improvement in the population hybrid and extracted hybrids.

There is the risk that the improvement in the populations may be specific to the inbred tester used. This problem could be circumvented by changing the inbred testers periodically. A logical approach would be to replace the inbred testers with inbreds isolated from successively improved selection populations.

The inbred tester modification has a practical advantage in that superior hybrid genotypes can be identified directly from reciprocal recurrent selection. Genotypes with good testcross performance could be saved for further selfing and testcrossing with the tester lines.

SUMMARY

Seven cycles of reciprocal recurrent selection for grain yield have been completed in the BSSS(R) and BSCB1(R) maize populations. The C_0, C_1, C_3, C_5, and C_7 selection cycle populations of BSSS(R) and BSCB1(R) and the C_0xC_0, C_5xC_5, and C_7xC_7 population crosses and two check entries were evaluated in six environments with five replications in each environment.

A computer program was written to simulate reciprocal recurrent selection as it is done under field conditions with maize. The two simulated populations consisted of 110 genotypes each with 40 independently segregating loci with two alleles. Testcrosses were formed by mating one male with four random females from the opposite population. An environmental deviate, chosen to be an independent, normally distributed variable with mean zero and variance 100, was added to each half-sib family mean to maintain a low heritability. The 11 (10%) superior lines were recombined to form the new selection populations. Six different starting conditions were obtained by imposing three levels of dominance at each of two different gene frequencies in the initial populations. Ten cycles of reciprocal recurrent selection were simulated, and duplicate runs were made for each starting condition.

A 1.75 q/ha per cycle increase in grain yield was realized in the BSSS(R)Cn x BSCB1(R)Cn cross, but the yield of the

populations themselves did not change significantly with cycles of selection. Significant changes in some other agronomic traits were noted in the populations themselves and the population crosses.

Heritability values for grain yield have not changed appreciably over cycles of selection in either population. Selection of male parents from among S_1 plants rather than from among S_0 plants has increased the variation among test-cross entries. Although the yield of the source populations was not improved, the genotypic variance remained the same for the successive cycles of selection.

Predicted gains from reciprocal recurrent selection were calculated from the variance component estimates. Observed gains were considerably less than predicted gains.

In the simulation studies rates of improvement were greater in the population hybrid than in the populations themselves with partial and complete dominance. With no dominance hybrid improvement was midway between improvement rates in the populations themselves. Although rate and total improvement were greatest for the no dominance condition, highest hybrid means were obtained with complete dominance.

Both the field and simulation studies showed that reciprocal recurrent selection can improve hybrid performance. However, it is not an efficient method to improve the populations themselves when the trait is controlled by loci with partial to complete dominance.

Genotypic variances were higher than their theoretical expectations in the simulated populations. This was probably because only one male was sampled from each S_1 line. Genotypic variances declined with cycles of selection resulting in a curvilinear response to selection in the simulated populations and population crosses for all starting conditions. Predicted gains from simulated reciprocal recurrent selection were calculated from the observed variance components. Predicted advances greatly exceeded observed gains from selection for all conditions.

Heterosis increased with cycles of selection in the field and in the simulation studies when partial or complete dominance was imposed. From these results it was concluded that reciprocal recurrent selection has improved the source populations in a complementary fashion to maximize hybrid performance.

The highest correlation between simulated and field results was obtained with complete dominance and equal gene frequencies in the simulated populations. It was concluded the BSSS(R) and BSCB1(R) populations have similar mean gene frequencies and that most of the improvement for grain yield in the hybrid can be explained by a model with partial to complete dominance at most loci.

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APPENDIX A

Explanation of Abbreviations Used in Appendix Tables

Abbreviation	Description
YLD	Grain yield (q/ha)
DS	Day after July 1, to 50% silk
PH	Plant height (cm)
EH	Ear height (cm)
TH	Top height (cm)
EL	Ear length (cm)
ED	Ear diameter (cm)
CD	Cob diameter (cm)
KD	Kernel depth (cm)
EARPNT	Ears per plant
KW	Weight of 300 kernels (g)

Table 43. Linear regression coefficients of genotypic means with cycles of selection for each duplicate run

Starting condition	Population	1	2
1	A	0.33±0.31	0.87±0.40
	B	0.78±0.31	0.08±0.40
	AB	3.63±0.31	3.09±0.40
2	A	1.71±0.19	2.27±0.21
	B	2.51±0.19	1.41±0.21
	AB	3.91±0.19	3.54±0.21
3	A	6.76±0.47	5.54±0.39
	B	4.31±0.47	3.85±0.39
	AB	5.56±0.47	4.70±0.39
4	A	2.65±0.27	0.20±0.31
	B	1.74±0.27	2.85±0.31
	AB	5.23±0.27	5.03±0.31
5	A	3.14±0.26	2.69±0.32
	B	2.20±0.26	3.05±0.32
	AB	4.61±0.26	5.10±0.32
6	A	6.42±0.34	5.29±0.25
	B	4.41±0.34	4.42±0.25
	AB	5.39±0.34	4.93±0.25

Table 44. Linear and quadratic regression coefficients of genotypic means with cycles of selection for each duplicate run

Starting condition	Population	1	2
1	A	3.78±0.67[a]	3.63±0.87
		-0.35±0.06[b]	-0.28±0.08
	B	1.10±0.67	3.77±0.87
		-0.03±0.06	-0.37±0.08
	AB	6.84±0.67	7.12±0.87
		-0.34±0.06	-0.40±0.08
2	A	2.58±0.66	3.57±0.53
		-0.09±0.06	-0.13±0.05
	B	3.15±0.66	2.97±0.53
		-0.06±0.06	-0.16±0.53
	AB	4.87±0.66	5.68±0.53
3	A	12.43±0.57	9.61±0.88
		-0.57±0.05	-0.41±0.08
	B	8.05±0.57	6.50±0.88
		-0.37±0.05	-0.26±0.08
	AB	10.30±0.57	8.20±0.88
		-0.47±0.05	-0.35±0.08
4	A	2.51±0.69	-0.16±0.67
		0.01±0.07	0.04±0.06
	B	4.29±0.69	5.36±0.67
		-0.25±0.07	-0.25±0.06
	AB	8.13±0.69	9.10±0.67
		-0.30±0.07	-0.41±0.06
5	A	4.68±0.64	4.94±0.50
		-0.15±0.06	-0.23±0.05
	B	4.16±0.64	5.86±0.50
		-0.20±0.06	-0.28±0.05
	AB	7.32±0.64	9.32±0.50
		-0.27±0.06	-0.42±0.05
6	A	10.41±0.54	5.70±0.60
		-0.40±0.05	-0.04±0.06
	B	7.20±0.54	7.67±0.60
		-0.28±0.05	-0.32±0.06
	AB	8.68±0.54	6.82±0.60
		-0.33±0.05	-0.19±0.06

[a] Linear regression coefficient.

[b] Quadratic regression coefficient.

Table 45. Estimates of phenotypic variance (σ_P^2) and genotypic variance (σ_G^2) in populations A and B and predicted and actual gain in each cycle of selection for starting condition 1

Selection cycle	Population A		Population B		Hybrid improvement	
	σ_P^2	σ_G^2	σ_P^2	σ_G^2	Predicted	Actual
0	173.2	53.5	159.1	51.4		
1	145.7	44.9	161.8	35.7	20.4	8.0
2	146.8	26.8	142.6	28.9	17.0	7.2
3	156.8	36.5	126.3	28.7	12.9	4.1
4	131.2	24.2	139.6	20.2	14.6	5.5
5	122.4	16.4	135.9	16.4	10.9	3.4
6	117.4	15.0	125.2	14.3	8.6	2.0
7	134.1	10.3	111.6	9.7	7.9	2.6
8	112.8	10.2	105.7	5.7	5.7	1.0
9	121.1	8.1	108.5	7.6	4.8	2.4
					4.6	0.4

Table 46. Estimates of phenotypic variance (σ_P^2) and genotypic variance (σ_G^2) in populations A and B and predicted and actual gains from each cycle of selection for starting condition 2

Selection cycle	Population				Hybrid improvement	
	A		B			
	σ_P^2	σ_G^2	σ_P^2	σ_G^2	Predicted	Actual
0	161.3	41.7	160.2	43.6		
1	145.0	33.3	137.8	33.2	17.5	6.3
2	126.4	27.3	155.4	34.9	14.9	5.2
3	132.0	25.4	142.5	26.5	14.1	3.3
4	128.4	19.3	123.7	22.6	12.3	3.9
5	118.5	17.7	148.4	18.3	10.7	3.0
6	124.5	17.5	120.9	12.5	9.2	4.8
7	121.0	15.3	119.1	13.5	8.1	4.0
8	110.3	7.8	118.7	7.1	7.9	3.3
9	121.2	8.1	115.1	6.6	4.4	1.9
					4.3	1.5

Table 47. Estimates of phenotypic variance (σ_P^2) and genotypic variance (σ_G^2) in populations A and B and predicted and actual gains from each cycle of selection for starting condition 3

Selection cycle	Population A		Population B		Hybrid improvement	
	σ_P^2	σ_G^2	σ_P^2	σ_G^2	Predicted	Actual
0	217.1	41.4	150.8	37.0		
1	142.0	36.5	148.6	25.1	15.9	8.6
2	129.0	28.4	174.4	30.4	13.9	7.5
3	146.0	27.6	155.8	24.2	13.3	5.9
4	146.1	29.2	143.8	27.8	12.0	6.0
5	128.7	27.5	145.9	23.2	13.1	9.0
6	143.1	14.3	119.6	15.9	12.2	4.3
7	144.8	12.0	130.6	11.7	8.0	4.0
8	115.1	10.2	125.8	13.6	6.3	2.5
9	108.8	9.8	125.8	12.4	6.6	1.9
					6.3	0.8

Table 48. Estimates of phenotypic variance (σ_P^2) and genotypic variance (σ_G^2) in populations A and B and predicted and actual gains from each cycle of selection for starting condition 4

Selection cycle	Population				Hybrid improvement	
	A		B			
	σ_P^2	σ_G^2	σ_P^2	σ_G^2	Predicted	Actual
0	171.7	46.9	223.3	92.0		
1	171.7	45.0	186.6	57.1	23.7	9.6
2	139.2	34.6	165.6	59.1	19.6	7.1
3	136.8	26.7	163.4	56.7	18.9	7.3
4	139.2	17.8	139.7	44.7	17.1	6.1
5	117.1	20.8	136.1	43.4	14.0	5.0
6	133.6	21.7	157.2	34.5	14.7	3.8
7	121.6	13.6	140.5	25.1	12.8	4.0
8	120.3	11.2	121.3	16.7	9.7	4.8
9	108.7	11.3	144.1	12.6	7.7	2.5
					6.5	1.5

Table 49. Estimates of phenotypic variance (σ_P^2) and genotypic variance (σ_G^2) in populations A and B and predicted and actual gains from each cycle of selection for starting condition 5

Selection cycle	Population				Hybrid improvement	
	A		B			
	σ_P^2	σ_G^2	σ_P^2	σ_G^2	Predicted	Actual
0	172.6	39.4	205.9	70.7		
1	123.8	32.3	165.4	55.5	20.2	10.2
2	137.7	38.3	149.7	43.5	18.3	6.4
3	153.2	25.6	139.1	41.0	17.4	6.3
4	138.7	20.9	179.2	33.6	14.7	5.7
5	138.4	20.0	149.9	25.6	12.2	5.3
6	124.7	19.9	104.7	17.8	10.9	4.4
7	140.9	18.7	137.9	20.1	10.0	3.2
8	158.1	12.1	120.8	12.6	9.7	3.8
9	124.8	8.3	105.2	10.0	6.5	2.7
					5.3	1.6

Table 50. Estimates of phenotypic variance (σ_P^2) and genotypic variance (σ_G^2) in populations A and B and predicted and actual gain from each cycle of selection for starting condition 6

Selection cycle	Population				Hybrid improvement	
	A		B			
	σ_P^2	σ_G^2	σ_P^2	σ_G^2	Predicted	Actual
0	170.6	28.2	137.7	34.9		
1	146.2	36.1	144.1	35.9	14.0	5.7
2	133.8	41.8	183.3	36.8	15.8	7.4
3	150.0	28.0	135.1	35.2	16.6	6.9
4	125.8	21.3	121.9	23.3	14.4	7.4
5	123.8	20.9	118.8	20.8	11.3	4.9
6	129.6	16.6	122.2	20.1	10.7	3.8
7	159.3	18.1	122.1	23.4	9.6	4.7
8	135.8	17.0	128.6	16.9	10.2	2.5
9	110.1	16.0	110.7	15.4	8.8	5.2
					8.7	2.6

Table 51. Mean values for all traits measured in environment 1

Entry	YLD	DS	PH	EH	TH	EL	ED	CD	KD	EARPNT	KW
1	57.0	23.0	210.6	115.1	95.4	18.0	5.0	2.9	2.1	1.1	81.3
2	59.4	22.2	201.4	106.3	95.2	17.5	4.8	2.8	2.0	1.2	77.1
3	59.1	19.8	202.9	102.7	100.2	17.8	4.7	2.8	1.9	1.1	80.5
4	64.3	20.8	210.0	103.7	106.3	19.1	4.8	3.0	1.9	1.3	81.8
5	62.2	21.4	212.8	107.3	105.5	18.7	4.7	2.9	1.8	1.2	79.6
6	57.8	17.2	211.1	99.4	111.6	20.2	4.6	2.9	1.7	1.1	69.3
7	62.0	17.4	215.5	103.3	112.2	19.2	4.6	2.9	1.7	1.2	78.4
8	62.6	19.4	207.0	103.7	103.3	20.5	4.6	2.9	1.7	1.2	70.8
9	61.2	19.4	196.8	96.6	100.2	20.2	4.4	2.9	1.5	1.2	70.2
10	56.4	20.8	207.5	96.9	110.6	18.5	4.5	2.8	1.7	1.2	73.2
11	64.6	20.2	224.3	121.5	102.7	19.6	4.8	2.9	2.0	1.1	85.3
12	67.3	22.2	201.3	115.1	86.2	17.7	4.6	2.8	1.8	1.4	88.5
13	58.8	26.8	250.3	146.3	104.0	18.2	5.0	3.0	2.0	1.0	83.8
14	82.4	19.6	227.7	118.2	109.5	19.3	4.8	2.9	1.9	1.5	82.6
15	85.2	19.0	230.1	110.6	119.5	20.2	4.9	2.9	2.0	1.3	85.1

Table 52. Mean values for all traits measured in environment 2

Entry	YLD	PH	EH	TH	EL	ED	CD	KD	EARPNT	KW
1	43.2	200.4	103.1	97.4	17.4	4.8	2.9	1.9	0.9	78.9
2	43.9	189.5	94.1	95.4	17.3	4.7	2.8	1.9	1.0	75.7
3	42.1	186.9	89.3	97.6	17.7	4.7	2.9	1.7	1.0	76.5
4	43.0	195.6	91.5	104.1	18.2	4.7	2.9	1.8	1.0	78.6
5	43.9	199.2	96.6	102.6	17.5	4.6	2.9	o.8	1.1	81.2
6	43.6	185.5	84.4	101.2	19.3	4.5	2.8	1.7	1.0	69.4
7	44.8	188.0	85.0	103.0	17.9	4.5	2.8	1.7	1.0	67.8
8	47.0	191.3	86.6	104.7	19.0	4.6	2.9	1.7	1.0	72.5
9	44.9	183.9	84.5	99.4	20.2	4.5	3.0	1.5	1.1	68.0
10	41.0	182.1	76.0	106.1	19.1	4.5	2.8	1.6	1.1	76.9
11	51.7	203.9	99.9	103.9	19.0	4.7	2.9	1.7	1.0	80.5
12	46.8	182.1	92.1	90.1	18.5	4.6	3.0	1.6	1.1	86.5
13	45.2	217.5	122.7	94.8	18.7	4.9	3.1	1.8	1.0	80.3
14	56.6	204.6	100.4	104.2	19.7	4.8	3.1	1.7	1.1	77.7
15	58.5	209.3	98.3	110.9	19.3	4.7	2.9	1.9	1.1	81.5

Table 53. Mean values for all traits measured in environment 3

Entry	YLD	PH	EH	TH	EL	ED	CD	KD	EARPNT	KW
1	66.9	182.4	97.1	85.4	17.6	4.8	3.0	1.9	0.9	87.7
2	54.3	173.5	88.4	85.0	16.5	4.6	2.8	1.8	0.9	79.0
3	64.5	172.9	88.2	84.8	17.5	4.6	2.8	1.8	1.0	82.2
4	76.6	187.3	92.7	94.6	18.5	4.7	2.9	1.8	1.0	88.5
5	61.0	184.0	89.8	94.1	18.3	4.7	2.9	1.8	1.0	87.2
6	69.3	180.1	87.3	92.8	19.5	4.6	2.8	1.7	1.0	77.5
7	68.7	177.6	83.4	94.2	19.5	4.6	2.9	1.7	1.0	78.2
8	65.8	180.3	82.6	97.6	20.3	4.5	2.9	1.5	0.9	77.2
9	65.8	178.4	86.6	91.8	19.1	4.5	3.0	1.5	1.0	79.9
10	60.1	176.6	81.9	94.8	18.8	4.5	2.8	1.7	1.0	84.8
11	75.2	186.9	95.3	91.5	19.2	4.6	2.9	1.7	1.0	80.7
12	70.0	165.2	87.8	77.4	18.1	4.7	2.9	1.7	1.0	93.8
13	57.9	200.1	112.2	87.9	18.2	4.8	3.0	1.8	0.9	89.6
14	88.2	194.8	100.1	94.8	20.9	4.9	3.0	1.9	1.1	88.0
15	91.5	200.3	96.1	104.2	20.2	4.8	2.9	1.9	1.1	89.4

Table 54. Mean values for all traits measured in environment 4

Entry	YLD	DS	PH	EH	TH	EL	ED	CD	KD	EARPNT	KW
1	51.1	28.6	191.2	90.5	100.7	16.5	4.6	2.8	1.8	0.9	73.9
2	50.8	26.8	179.4	83.0	96.4	16.3	4.5	2.7	1.8	1.0	67.0
3	46.6	24.8	173.7	77.8	96.0	15.9	4.4	2.7	1.7	1.0	68.5
4	53.7	27.0	190.2	78.1	112.1	17.7	4.5	2.8	1.7	1.0	72.7
5	51.9	24.6	187.2	77.4	109.8	16.8	4.4	2.7	1.7	1.0	72.0
6	43.9	21.8	177.0	76.4	100.7	16.4	4.3	2.6	1.7	1.0	63.1
7	40.7	24.0	177.9	75.4	102.5	16.6	4.2	2.6	1.5	0.9	66.7
8	45.2	25.8	174.0	75.5	98.5	17.8	4.1	2.7	1.4	1.1	63.6
9	44.3	24.8	175.9	75.2	100.8	19.2	4.3	2.7	1.6	1.0	64.7
10	43.1	24.0	172.7	70.7	102.0	16.7	4.2	2.6	1.6	1.0	67.1
11	54.6	24.8	188.3	85.3	103.0	17.8	4.5	2.7	1.8	1.0	71.8
12	56.6	28.2	180.5	86.8	93.7	13.6	4.5	2.9	1.7	1.1	71.6
13	55.6	29.2	215.1	109.0	106.1	18.3	4.7	2.8	1.9	1.1	69.3
14	62.3	23.8	193.0	85.3	107.7	19.3	4.5	2.9	1.7	1.0	70.6
15	66.7	22.6	197.7	85.2	112.5	18.5	4.6	2.7	1.9	1.0	77.4

Table 55. Mean values for all traits measured in environment 5

Entry	YLD	PH	EH	TH	EL	ED	CD	KD	EARPNT	KW
1	14.4	198.8	96.9	101.9	13.1	3.8	2.4	1.4	0.6	63.9
2	21.5	191.1	89.9	101.2	13.6	3.9	2.5	1.3	0.8	65.1
3	28.7	187.4	85.7	101.8	14.4	4.1	2.6	1.6	0.9	69.9
4	23.0	201.4	89.0	112.4	14.7	4.0	2.7	1.3	0.8	70.4
5	25.1	197.2	87.1	110.1	15.1	4.2	2.7	1.5	0.8	69.8
6	24.6	185.7	81.7	104.0	15.5	3.9	2.6	1.4	0.7	62.4
7	25.2	177.4	75.1	102.3	15.2	3.9	2.6	1.3	0.7	59.9
8	31.9	186.8	77.5	109.3	17.2	4.0	2.6	1.3	0.9	62.0
9	23.8	174.7	73.5	101.2	16.0	3.8	2.5	1.3	0.8	61.2
10	25.5	179.3	69.2	110.1	15.4	3.7	2.4	1.3	0.9	68.8
11	24.8	195.2	88.5	106.7	16.2	3.9	2.5	1.3	0.7	70.0
12	23.1	181.9	87.1	94.8	14.4	3.9	2.6	1.3	0.8	66.4
13	24.4	225.3	118.5	106.8	15.8	4.2	2.7	1.5	0.7	70.1
14	29.6	201.9	87.5	114.4	16.7	3.8	2.6	1.2	0.8	67.9
15	35.3	205.8	86.4	119.4	16.2	4.0	2.6	1.4	0.9	71.4

Table 56. Mean values for all traits measured in environment 6

Entry	YLD	PH	EH	TH	EL	ED	CD	KD	EARPNT	KW
1	66.9	217.2	103.6	113.6	18.3	4.9	2.9	2.0	0.9	81.9
2	64.7	199.2	97.3	102.0	18.0	4.6	2.7	1.9	1.0	75.7
3	68.3	198.2	93.1	105.1	17.2	4.6	2.8	1.9	1.1	79.3
4	69.0	212.2	94.6	117.6	18.2	4.6	2.9	1.8	1.0	81.0
5	70.5	211.9	91.7	120.2	17.7	4.7	2.8	1.9	1.1	83.0
6	72.2	214.5	101.4	113.1	19.5	4.6	2.8	1.8	1.0	72.2
7	66.7	207.9	94.5	113.4	19.0	4.6	2.8	1.8	1.1	67.5
8	66.5	211.5	101.2	110.3	19.8	4.5	2.8	1.7	1.0	68.9
9	62.1	201.4	93.2	108.3	19.9	4.3	2.6	1.7	1.0	70.1
10	58.5	202.3	87.2	115.2	17.8	4.4	2.7	1.6	1.0	72.3
11	80.2	223.3	106.2	117.1	19.7	4.8	2.9	1.9	1.0	80.7
12	69.2	200.6	100.0	100.6	17.6	4.8	2.9	1.9	1.1	90.5
13	84.7	249.3	131.6	117.7	18.9	4.9	3.0	2.0	1.1	86.0
14	85.1	226.2	107.8	118.4	20.6	4.8	2.9	1.9	1.1	80.5
15	86.6	227.2	104.2	123.0	20.4	4.8	2.9	1.9	1.1	85.4

APPENDIX B

Source Listing of Computer Simulation Program

```
VAR: PROCEDURE OPTIONS(MAIN) REORDER ;
   DECLARE
   N /*NUMBER IN EACH POPN*/
   BINARY FIXED(31,0) ,
   C /* NUMBER OF CYCLES*/
   BINARY FIXED(31,0) ,
   TPCRS /* NUMBER OF TESTCROSSES*/
   BINARY FIXED(31,0) ,
   F /* NUMBER OF FEMALES MATED TO ONE  MALE*/
   BINARY FIXED(31,0) ,
   NPRGNY /* NUMBER OF OFFSPRING PER MATING IN RECOMBINATION*/
   BINARY FIXED(31,0) ,
   NLINE /* NUMBER OF LINES RECOMBINED*/
   BINARY FIXED(31,0) ,
   AX /* AMOUNT EACH LOCI ADDS */
   BINARY FIXED(31,0) ,
   D /* LEVEL OF DOMINANCE */
   DEC FLOAT(6) ,
   S2 /* PHENOTYPIC VARIANCE */
   DEC FLOAT(6) ,
   JMM /* NUMBER OF SEEDS*/
   BINARY FIXED(31,0) ,
   Z /* NUMBER OF UNIFORM RANDOM NUMBERS */
   BINARY FIXED(31,0) ,
   X /* NUMBER OF UNIFORM RANDOM NUMBERS */
   BINARY FIXED(31,0) ,
   ND /* NUMBER OF NORMAL DEVIATED */
   BINARY FIXED(31,0) ;
   GET EDIT(N,TPCRS,F,NPRGNY,NLINE)
   (F(5,0)) ;
   PUT EDIT(N,TPCRS,F,NPRGNY,NLINE)
   (F(5,0)) ;
   GET SKIP EDIT(C,AX,D,S2)
   (F(5,0),F(5,0),F(5,2),F(5,0)) ;
   PUT SKIP EDIT(C,AX,D,S2)
   (F(5,0),F(5,0),F(5,2),F(5,0)) ;
   GET SKIP EDIT(JMM,Z,X,ND)
   (F(5,0)) ;
   PUT SKIP EDIT(JMM,Z,X,ND)
   (F(5,0)) ;
   GET SKIP ;
   CALL SIM ;
            /*MAIN PROGRAM */
SIM: PROCEDURE ;
   DECLARE
   (SS(N,2), CB(N,2)) /* ARRAYS OF POPNS */
   BIT(40),
   SL(TPCRS,2) /* HOLDING ARRAY*/
   BIT(40),
   (STORSS(40,0:C),STORCB(40,0:C))   /*ARRAY OF FREQUENCIES*/
```

```
DEC FLOAT(6) ,
(GGUB,GGNOR) EXTERNAL ENTRY OPTIONS (FORTRAN) ,
PRGNY(TPCRS,F) /* ARRAY WITH TESTCROSS INFO*/
DEC FLOAT(6) ,
INFO(0:C,6) /* ARRAY WITH POPN INFO */
DEC FLOAT(6) ,
SELCT(NLINE,2) /* ARRAY OF SELECTED INDIVIDUALS*/
BIT(40) ,
UN(Z) /* ARRAY OF RANDOM NUMBERS*/
DEC FLOAT(6) ,
(NWRD,NBIT,LOCI)
BINARY FIXED(31,0) ,
(I,J,ICHK)
FIXED,
CYCLE
FIXED ,
(SEED(JMM),ISEED,THRO,T)
BINARY FIXED(31,0) ,
CROSS
DEC FLOAT(6),
RECIP
FIXED ,
TEMP
BIT(40) ,
ERROR FIXED(1);
NWRD = 2 ;
NBIT = 20;
LOCI = NWRD*NBIT;
          /*BRING IN POPULATIONS*/
DO I = 1 TO N ;
DO J = 1 TO 2 ;
GET EDIT(SS(I,J))
(B(LOCI)) ;
PUT SKIP EDIT(SS(I,J))
(B(LOCI)) ;
END;
END;
PUT SKIP ;
DO I = 1 TO N;
DO J = 1 TO 2 ;
GET EDIT(CB(I,J))
(B(LOCI)) ;
PUT SKIP EDIT(CB(I,J))
(B(LOCI)) ;
END ;
END ;
PUT SKIP LIST('EACH LOCI ADDS');
PUT EDIT(AX) (X(2),F(2));
PUT SKIP LIST('LEVEL OF DOMINANCE');
PUT EDIT(D) (X(2),F(4,2));
```

```
   DO CYCLE=0 TO C ;
   CALL POPN ;
   THRO=1;
   GET EDIT((SEED(I) DO I = 1 TO JMM)) (F(2));
   RECIP = 0 ;
            /*CALL THE PROCEDURE TO FORM THE TESTCROSSES*/
   CROSS=0 ;
   CALL TST ;
            /*CALL THE PROCEDURE TO EVALUATE THE TESTCROSSES*/
   IF CYCLE < C THEN
   CALL EVAL ;
   RECIP = 0 ;
   DO I = 1 TO N ;
   DO J = 1 TO 2 ;
   TEMP = SS(I,J) ;
   SS(I,J) = CB(I,J) ;
   CB(I,J) = TEMP ;
   END ;
   END ;
   PUT SKIP ;
   CALL TST ;
   IF CYCLE < C THEN
   CALL RECOMB ;
   RECIP = 1 ;
   IF CYCLE < C THEN
   CALL EVAL ;
   IF CYCLE < C THEN
   CALL RECOMB ;
   CROSS=CROSS/(TPCRS*F*2) ;
   INFO(CYCLE,5) = CROSS ;
   END;
   DO CYCLE=0 TO C ;
   PUT SKIP EDIT((INFO(CYCLE,J) DO J = 1 TO 5))
   (F(7,2),X(2),F(7,2),X(2),F(6,4),X(2),F(6,4),X(2),F(7,2)) ;
   PUT SKIP;
   END ;
   DO I = 1 TO 40 ;
   PUT SKIP EDIT((STORSS(I,J) DO J = 0 TO C ))
   (F(7,4)) ;
   END;
   PUT SKIP ;
   DO I = 1 TO 40 ;
   PUT SKIP EDIT((STORCB(I,J) DO J = 0 TO C))
   (F(7,4)) ;
   END;
            /*THIS PROCEDURE CALCULATES POPULATION PARAMETERS */
POPN: PROCEDURE ;
   DECLARE
   (I,J,L)
   BINARY FIXED(31,0) ,
```

```
(FLS,FLC,INDS,INDC,POPS,POPC,FREQS,FREQC,STOR(LOCI,2))
DEC FLOAT(6) ,
SRCH
BIT(1) ;
POPS = 0 ;
POPC = 0 ;
DO L = 1 TO LOCI ;
DO J = 1 TO 2 ;
STOR(L,J) = 0 ;
END ;
END ;
DO I = 1 TO N ;
INDS = 0 ;
INDC = 0 ;
DO L=1 TO LOCI ;
FLS = 0 ;
FLC = 0 ;
DO J = 1 TO 2 ;
SRCH = SUBSTR(SS(I,J),L,1) ;
IF SRCH = '1'B THEN FLS = FLS + 1 ;
SRCH = SUBSTR(CB(I,J),L,1) ;
IF SRCH = '1'B THEN FLC =FLC+1 ;
END ;
IF FLS = 2 THEN
INDS = INDS + FLS*AX ;
ELSE
INDS = INDS + FLS*AX + FLS*AX*D ;
IF FLC = 2 THEN
INDC = INDC + FLC*AX ;
ELSE
INDC = INDC + FLC*AX + FLC*AX*D ;
STOR(L,1) = STOR(L,1) + FLS ;
STOR(L,2) = STOR(L,2) + FLC ;
END ;
POPS = POPS + INDS ;
POPC = POPC + INDC ;
END ;
FREQS = 0 ;
FREQC = 0 ;
DO L = 1 TO LOCI ;
STOR(L,1) = STOR(L,1)/(2*N) ;
STORSS(L,CYCLE)=STOR(L,1) ;
FREQS = FREQS + STOR(L,1) ;
STOR(L,2) = STOR(L,2)/(2*N) ;
STORCB(L,CYCLE)=STOR(L,2) ;
FREQC = FREQC + STOR(L,2) ;
END ;
POPS = POPS/N ;
POPC = POPC/N ;
INFO(CYCLE,1)=POPS;
```

```
     INFO(CYCLE,2)=POPC ;
     PUT SKIP LIST('AVERAGE OF POPULATIONS');
     PUT SKIP EDIT(POPS,POPC)
     (F(7,3),X(3),F(7,3)) ;
     FREQS=FREQS/LOCI;
     FREQC=FREQC/LOCI;
     INFO(CYCLE,3)=FREQS ;
     INFO(CYCLE,4)=FREQC ;
     PUT SKIP LIST('END OF POPN PROCEDURE') ;
     RETURN ;
     END POPN ;
/*THIS PROCEDURE FORMS TESTCROSS PROGENY*/
  TST: PROCEDURE ;
     DECLARE
     (GMTM,GMTF)
     BIT(40),
     (AND,OR,HET,A1(2))
     FIXED BINARY(20),
     (NUM,I,II,K,AD1,AD2,DOM,DMT,P,W,L)
     BINARY FIXED(31,0) ,
     UNRN(X)
     DEC FLOAT(6) ,
     TASSEL
     FIXED ,
     (B(2),C(2))
     BIT(40);
     AD1,AD2,DOM=0;
              /*BRING IN UNIFORM RANDOM NUMBERS*/
     ISEED = SEED(THRO) ;
     CALL GGUB(ISEED,X,UNRN) ;
     THRO=THRO+1;
     NUM = 0 ;
     DO I = 1 TO TPCRS ;
     K=I;
     ISEED = SEED(THRO) ;
     CALL GGUB (ISEED,Z,UN) ;
     THRO=THRO+1;
     T=1 ;
     B(1) = SS(K,1) ;
     B(2) = SS(K,2) ;
     TASSEL = 0 ;
     CALL SELF ;
     PUT SKIP ;
     DO II = 1 TO F ;
     NUM = NUM + 1 ;
     K = UNRN(NUM)*N+1 ;
     C(1) = CB(K,1) ;
     C(2) = CB(K,2) ;
     GMTF = (40)'0'B;
     TASSEL = 1 ;
```

```
  GMTM = (40)'0'B ;
  CALL GAM(GMTM,B) ;
            /*MATE ONE MALE TO F FEMALES*/
            /*CALL THE PROCEDURE TO PRODUCE A RANDOM GAMETE*/
  CALL GAM(GMTF,C) ;
  AD1,AD2,DMT =0 ;
            /*COUNT THE FAVORABLE ALLELES IN EACH GAMETE */
  CALL KOUNT(GMTM,AD1);
  CALL KOUNT(GMTF,AD2);
            /*GO THROUGH STEPS TO COUNT HETEROZYGOUS LOCI*/
  P = 1 ;
  DO W = 1 TO NWRD ;
  A1(1)=SUBSTR(GMTM,P,NBIT);
  A1(2)=SUBSTR(GMTF,P,NBIT);
  AND = ALL(A1);
  OR  = ANY(A1);
  HET = OR - AND ;
            /*CALL THE PROCEDURE TO COUNT THE NO. OF HETEROZYGOTES
              IN EACH SEGMENT OF LENGTH NBIT*/
  CALL SHORT(DOM);
  DMT = DMT + DOM;
  P = P + NBIT ;
  END ;
  PRGNY(I,II) = (AD1+AD2)*AX +AX*DMT*D ;
  CROSS = PRGNY(I,II) + CROSS ;
  END ;
  PUT LIST(I);
  END ;
  DO I = 1 TO TPCRS ;
  PUT SKIP ;
  PUT EDIT((PRGNY(I,II) DO II = 1 TO F)) (F(6,0)) ;
  END ;
  RETURN ;
            /*THIS PROCEDURE SELFS AN INDIVIDUAL AND PRODUCES A RAN
              DOM GAMETE FROM THE SELFED INDIVIDUAL*/
            /* THIS PROCEDURE SELFS THE MALE AND STORES
               THE SELFED INDIVIDUAL. RANDOM GAMETES ARE PRODUCED
               FROM THE SELFED INDIVIDUAL */
SELF: PROCEDURE ;
  DECLARE
  (S,Q)
  FIXED ;
  DO S = 1 TO 2 ;
  DO Q = 1 TO LOCI ;
  IF UN(T) < 0.5 THEN
  SUBSTR(SL(I,S),Q,1)=SUBSTR(B(1),Q,1) ;
  ELSE
  SUBSTR(SL(I,S),Q,1) = SUBSTR(B(2),Q,1) ;
  T = T + 1 ;
  END ;
```

```
   END ;
   B(1) = SL(I,1) ;
   B(2) = SL(I,2) ;
   RETURN ;
END SELF ;
GAM: PROCEDURE(GMT,A) ;
   DECLARE
   GMT
   BIT(40) ,
   A(2)
   BIT(40) ,
   Q
   FIXED ;
   DO Q = 1 TO LOCI ;
   IF UN(T) < 0.5 THEN
   SUBSTR(GMT,Q,1) = SUBSTR(A(1),Q,1) ;
   ELSE
   SUBSTR(GMT,Q,1) = SUBSTR(A(2),Q,1) ;
   T = T + 1 ;
   END ;
   RETURN ;
END GAM ;
            /* THIS PROCEDURE COUNTS THE NUMBER OF 1'S IN A
               BIT STRING */
KOUNT: PROCEDURE(GMT,FREQ);
   DECLARE
   (P,P1,FREQ)
   BINARY FIXED(31,0) ,
   GMT
   BIT(40),
   SRCH BIT(1) INITIAL ('1') ;
   P,P1 = INDEX(GMT,SRCH) ;
   DO FREQ = 0 BY 1 WHILE(P¬=0);
   P = INDEX(SUBSTR(GMT,P1 + 1),SRCH) ;
   P1 = P1 + P ;
   END ;
   RETURN ;
   END KOUNT ;
            /*THIS PROCEDURE COUNTS THE NO. OF 1'S IN A WORD*/
SHORT: PROCEDURE(FREQ);
   DECLARE
   (P,P1,FREQ)
   BINARY FIXED(31,0) ,
   SRCH BIT(1) INITIAL ('1') ;
   P1,P = INDEX(HET,SRCH) ;
   DO FREQ = 0 BY 1 WHILE(P¬=0);
   P = INDEX(SUBSTR(HET,P1+1),SRCH) ;
   P1 = P1 + P ;
   END ;
   RETURN ;
```

```
   END SHORT ;
   END TST ;
            /* THIS PROCEDURE EVALUATES THE TEST CROSSES */
EVAL: PROCEDURE ;
   DECLARE
   HSFM(TPCRS,2) /*ARRY OF HS GENOTYPIC AND PHENOTYPIC MEANS */
   DEC FLOAT(6),
   NDEV(ND) /*ARRAY OF NORMAL DEVIATES */
   DEC FLOAT(6) ,
   (I,J,L,N,Y)
   BINARY FIXED(31,0),
   (SRCH,VAR,V1,V2)
   DEC FLOAT(6) ;
   ISEED = SEED(THRO);
   CALL GGNOR(ISEED,ND,NDEV) ;
   THRO = THRO + 1 ;
   DO I = 1 TO TPCRS ;
   DO J = 1 TO 2 ;
   HSFM(I,J) = 0 ;
   END ;
   END ;
   Y =1 ;
   DO I = 1 TO TPCRS ;
   DO J = 1 TO F ;
   HSFM(I,1) = HSFM(I,1) + PRGNY(I,J) ;
   END ;
   HSFM(I,1) = HSFM(I,1)/F ;
   HSFM(I,2) = HSFM(I,1) + NDEV(Y)*S2;
   Y = Y + 1 ;
   END ;
   PUT SKIP LIST('TEST CROSS INFORMATION FOR CYCLE');
   PUT EDIT(CYCLE)
   (F(4)) ;
   DO I = 1 TO TPCRS ;
   PUT SKIP EDIT(HSFM(I,1),HSFM(I,2))
   (F(7,2), F(7,2));
   END ;
   /* CALCULATE VARIANCE */
   PUT SKIP LIST('VARIANCES');
   DO J=1 TO 2 ;
   V1 = 0 ;
   V2 = 0 ;
   VAR= 0 ;
   DO I = 1 TO TPCRS ;
   V1 = V1 + HSFM(I,J);
   V2 = V2 + HSFM(I,J)*HSFM(I,J) ;
   END ;
   V1 = (V1*V1)/TPCRS ;
   VAR= (V2-V1)/(TPCRS-1) ;
   PUT EDIT(VAR)
```

```
   (F(7,2));
   END ;
   /* PICK OUT BEST FAMILIES */
   DO L= 1 TO NLINE ;
   SRCH = 0 ;
   DO I = 1 TO TPCRS ;
   IF SRCH < HSFM(I,2) THEN
   DO
   SRCH = HSFM(I,2) ;
   N  = I ;
   END ;
   END ;
   IF CYCLE=0 THEN
   PUT SKIP EDIT(HSFM(N,2))
   (F(6,2)) ;
   HSFM(N,2) = 0 ;
   SELCT(L,1) = SL(N,1);
   SELCT(L,2) = SL(N,2);
   PUT SKIP;
   IF CYCLE=0 THEN
   PUT SKIP EDIT(SELCT(L,1))
   (B(40));
   IF CYCLE=0 THEN
   PUT SKIP EDIT(SELCT(L,2))
   (B(40));
   END;
   PUT SKIP LIST('EVAL COMPLETED') ;
   RETURN ;
END EVAL;
            /* THIS PROCEDURE RECOMBINES THE SELECTED LINES*/
 RECOMB: PROCEDURE ;
   DECLARE
   (I,J,K,L,M,W)
   FIXED ,
   A(2)
   BIT(LOCI),
   SWITCH
   FIXED ;
   L=1;
   DO I = 1 TO NLINE-1 ;
   K=I+1 ;
   DO  J = K TO NLINE ;
   A(1) = SELCT(I,1) ;
   A(2) = SELCT(I,2) ;
   SWITCH = 0 ;
   CALL GAMETE ;
   SWITCH = 1 ;
   L = L - NPRGNY ;
   A(1) = SELCT(J,1) ;
   A(2) = SELCT(J,2) ;
```

```
CALL GAMETE ;
END ;
END ;
IF RECIP = 0 THEN
DO ;
PUT SKIP LIST('NEW SS POPN');
DO M = 1 TO N ;
DO W = 1 TO 2 ;
PUT SKIP EDIT(SS(M,W))
(B(LOCI)) ;
END ;
END ;
END ;
ELSE DO ;
PUT SKIP LIST('THE NEW CB POPN') ;
DO M = 1 TO N ;
DO W = 1 TO 2 ;
PUT SKIP EDIT(CB(M,W))
(B(LOCI)) ;
END ;
END ;
END ;
          /* THIS PROCEDURE PRODUCES NPROGNY GAMETES FROM A
             SELFED INDIVIDUAL*/
GAMETE: PROCEDURE ;
DECLARE
GMT
BIT(40) ,
G(2)
BIT(40) ,
(S,Q)
FIXED;
ISEED = SEED(THRO) ;
CALL GGUB (ISEED,Z,UN) ;
THRO=THRO+1;
T = 1 ;
DO S = 1 TO 2 ;
DO Q = 1 TO LOCI ;
IF UN(T) < 0.5 THEN
SUBSTR(G(S),Q,1) = SUBSTR(A(1),Q,1) ;
ELSE
SUBSTR(G(S),Q,1) = SUBSTR(A(2),Q,1) ;
T = T + 1 ;
END ;
END ;
          /* THE S2 INDIVIDUAL IS STORED IN THE A ARRAY */
DO S = 1 TO 2 ;
A(S)=G(S);
END ;
          /* PRODUCE NPRGNY GAMETES FROM THE S2 */
```

```
    DO S = 1 TO NPRGNY ;
    DO Q = 1 TO LOCI ;
    IF UN(T) < 0.5 THEN
    SUBSTR(GMT,Q,1) = SUBSTR(A(1),Q,1) ;
    ELSE
    SUBSTR(GMT,Q,1) = SUBSTR(A(2),Q,1) ;
    T=T+1 ;
    END ;
    IF RECIP = 0 THEN
    DO ;
    IF SWITCH = 0 THEN
    SS(L,1) = GMT;
    ELSE
    SS(L,2) = GMT ;
    END ;
    ELSE DO ;
    IF SWITCH = 0 THEN
    CB(L,1) = GMT ;
    ELSE
    CB(L,2) = GMT ;
    END ;
    L = L + 1 ;
    END ;
    RETURN ;
 END GAMETE ;
END RECOMB ;
 END SIM ;
END VAR ;
```